TRANSIENT STRUCTURE IN BENTHIC COMMUNITIES
The Effects of Oxygen Stress, Burial and High Rates of Sedimentation

by

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Submitted to the Massachusetts Institute of Technology-Woods Hole Oceanographic Institution Joint Program in Biological Oceanography in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

The influence of natural short-term fluctuations in environmental parameters on three components of transient benthic invertebrate community structure: abundance of individuals and species, biomass of individuals, and species diversity, were investigated in this study. The effect of low dissolved-oxygen on transient benthic community structure was studied with samples from Golfo Dulce, an intermittently anoxic basin off the west coast of Costa Rica and the Fosa de Cariaco, an anoxoic trench off the north coast of Venezuela. Periodic fluctuations in oxygen concentration were accompanied by a community numerically dominated by a single polychaete species and low species diversity. As the frequency of fluctuations in oxygen concentration decreased, the number of species and individuals in the community increased with a corresponding increase in species diversity.

In contrast to fluctuating oxygen conditions which eliminated many species from the community, fluctuating amounts of suspended matter in the bottom water allowed one species to proliferate while maintaining the total species list length. High rates of terrigenious sedimentation occurring naturally off the Spanish Sahara coast produced conditions which apparently hampered the feeding mechanisms of a spionid polychaete. Further offshore, where the diversity should be expected to increase, the spionids were able to flourish. The result was greater numerical abundance and biomass offshore and a lower transient diversity value. Results of simulation of catastophic burial by in situ burial of small isolated portions of Buzzards Bay sediment indicated that sedimentation rates recorded off Spanish Sahara would not eliminate species by burial. However, the small size of the organisms found off Spanish Sahara is probably a result of the constant expenditure of energy for escape.

In regions of fluctuating environmental conditions, diversity values are low, principally because of dominance by a single species. Increasingly stable conditions, even though stressful, result in a more even distribution of individuals among the species present and a correspondingly high transient value.

Thesis Supervisor: Gilbert T. Rowe
Title: Associate Scientist

CHAPTER I

INTRODUCTION

The Community Concept

The concept of classifying the marine benthos into communities has been evolving for the past century. Mobius in 1877 generated the idea of biocoenosis: localized groupings of animals which reach equilibrium with their environment. He felt that the boundaries of a biocoenosis were determined by the biological relationships of the animals. Peterson (1913), after analyzing grab samples from Danish waters, proposed a statistical community concept. The most numerous, conspicious, and most "characteristic" species of animals were used to designate a community. This statistical classification did not rely on relationships between members of the community and their environment, nor place boundaries on the community. Peterson did contemplate the relationships between the members of his community but came to no conclusions. It remained to later workers to expand the "Peterson" community concept, particularly for the infauna, into one which emphasizes the significance of biological relationships rather than physical-chemical parameters of the environment. Allee et al. (1949) stated that "communities are composed not of random assortments of species, but of ecologically compatible species populations whose collective ecological requirements of food, shelter, and reproduction are satisified... by a certain range of environment".

This type of community concept is summarized in Thorson's (1957) parallel communities: communities, composed of the same genera are located in different regions. Such communities have been found in all oceans. Macoma communities have been described from the Arctic Ocean, Baltic Sea, N.E. Pacific Ocean, N.W. Pacific Ocean and Gulf of Mexico. Tellina communities from the North Sea, Mediterranean Sea, N.W. Atlantic Ocean, Gulf of Mexico and New Zealand waters. Venus communities have been found in the Arctic Sea, Japan Sea, Baltic Sea, North Sea, Mediterranean Sea, Black Sea, Persian Gulf, S.E. Atlantic Ocean and Florida waters and a Venus iso-community has been described from Menemsha Bight, Vineyard Sound, Mass. Amphiura communities and their iso-communities, Amphiodia-Amphioplus have been found in the Mediterranean Sea, North Atlantic Ocean, Black Sea, Japan Sea, S.W. Pacific Ocean, N.E. Pacific Ocean, S.E. Pacific Ocean and Persian Gulf. Foraminifera communities have been described from Arctic and North Sea waters (Thorson, 1957 and 1966). Thorson felt that a rather small number of genera dominated the infauna and thus studies of the ecology of a species from one area would provide an understanding of the ecological relationship in communities from other areas.

Further studies of warm water benthos have failed to find Peterson type communities. Instead of communities dominated by a few species, samples from California, Mexico, South Africa, S.E. Asia and Australian waters contained a large number of species represented by a few individuals (Stephensen, 1973). Stephensen, Williams and Lance (1970) stated that distributional patterns of the thirty-six most frequently occurring species in Moreton Bay, South Queensland showed only "ill-defined relationships" with their environment.

A major criticism of the "Peterson-type" community concept was that there did not exist any evidence for biological relationships among the animals. It was proposed that individual species were directly influenced by physical factors such as substrata (Lindroth, 1935). Jones (1950) suggested that the only consistent way to classify communities was on the basis of definite limits in the physical conditions of the environment. Such physical factors would be temperature, salinity, light, exposure to air and desiccation, available oxygen, nutrients, salts, hydrography, and substrata. Of these he felt temperature, salinity, and substrata to be the most important. On the basis of this he divided the Atlantic Ocean into four major groups of communities:

I. Arctic region. Temperature range -2 to 7°C

II. Atlantic boreal region. Temperature range 3 - 16°C

A. Shallow water and brackish communities
   1. Shallow soft-bottom biome
      (a) Shallow sand association
      (b) Shallow mud association
   2. Shallow hard-bottom biome
      (a) Shallow rock association
      (b) Shallow vegetation association

B. Offshore communities
   1. Offshore soft-bottom biome
      (a) Offshore sand association
      (b) Offshore muddy sand association
      (c) Offshore mud association
   2. Offshore hard-bottom biome
      (a) Offshore gravel association

C. Deep Communities
   1. Deep soft-bottom biome
      (a) Deep mud association
   2. Deep hard-bottom biome
      (a) Deep coral association

This classification of communities by biotope rather than biocoenosis is seldom used. It has influenced the work of Peres and Picard (1958). Their system of classification developed from work in the Mediterranean on both soft and hard substrates. Classification was based upon broad vertical subdivisions of the ocean, which were subdivided by biotope. Within each biotope division, communities were recognized either on a biotope or biocoenosis basis.

The concept of communities used in this study is one with no sharp delineations between groupings (Sanders, 1960; Wiser, 1960; and Mills, 1969). Communities are seen as shifts in

relative dominance of species within a continuous distribution pattern. The structure of the "continuum community" is influenced by both physical and biological factors. Mills (1969) summarized this concept by defining a community as: "a group of organisms occurring in a particular environment presumably interacting with each other and with the environment and separable by means of an ecological survey from other groups".

Community characteristics

Communities can be defined by their function and structure. Community function is concerned with the processes within the community and how they relate to an ecosystem. Function may have little to do with the composition of the community. Structure is the description of the division of the community among component species, their numerical abundance and their biomass. The present study is concerned with community structure.

Two related structural characteristics of benthic communities are abundance or density of individuals, and their weight (biomass) per unit volume or area of the bottom. Sanders and Hessler (1969) felt that density and biomass in the deep-sea benthos are controlled by available food since oxygen concentration, temperature, and sediment type did not show correlated changes or reach limiting levels. In a study off the north coast of Chile, Gallardo (1963) found

that low standing-crops of macrofauna correlated with oxygen concentrations. In the oxygen minimum region off Peru the benthos is composed of many individuals representing few taxa (Frankenberg and Menzies, 1968). They suggested that the proliferation of those species which tolerated low oxygen concentrations was due to the abundance of food in the sediments. Others have found little correlation between biomass and percent organic carbon in the sediment in the deep-sea (Sanders, Hessler, and Hampson, 1965; Rowe and Menzel, 1971), but biomass does correlate with surface productivity as long as critically low concentrations of oxygen are not reached (less than 5% saturation) (Rowe, 1971; Sanders, 1969). At sites of organic pollution with low dissolved oxygen in the bottom water and high organic carbon in the sediments, benthic species diversity is low and species composition is altered (Reish, 1956, 1959, 1970; Rowe, Polloni and Rowe, 1972; et al.).

Community biomass and animal abundance therefore appear to be proportional to the energy resources available to the community, unless some biological or physical phenomenon restricts them (Figure 1). What is not known is what these restrictions are, their mode of operation or how they influence the distribution of biomass among the individuals.

A third major parameter used to describe a community's structure is species-diversity: the number of species

present and their relative abundance. Numerous diversity indices have been proposed (Pielou, 1966; Sanders, 1968; Loucks, 1970; Hurlbert, 1971; Debendedictis, 1973). Two, Sanders rarefaction and Shannon-Wiener Information Function, are commonly used in benthic studies. The Shannon-Wiener Information Function (Shannon and Weaver, 1963) is used in this study to calculate diversity values of marine communities because it yields a single number, rather than a family of curves with which to work. The formula is:

$$H'(s) = -\sum p_i \log p_i$$

where p_i is the proportion of the i^{th} species in the population. This index estimates the average diversity of a community from the information (species number and abundance) obtained from a sample. The index was derived from "information theory" which states that the greater the information content (a measure of uncertainty), the greater the diversity. Its use implies that the population is too large for all individuals to be counted. Instead data are obtained from a random sample of the population which is assumed to be representative of the community (Pielou, 1966).

The usual practice in benthic studies has been to work only with a single taxon (Rex, 1973) or preferably several numerically dominant taxa, such as polychaetes and bivalves (Hessler and Sanders, 1967; Sanders, 1968; and Slobodkin and Sanders, 1969). This practice ignores the entire assemblage of organisms which are interacting with

energy-flow patterns in a community (Steele, 1974; Valentine, 1971). Diversity values based on numbers contained in a grab sample provide accurate descriptions of the community at one point in time. Several samples, taken within a short time span and treated individual, provide information on the homogeneity of an area.

Diversity based on biomass (which is a measure of the distribution of biomass among the species of an assemblage) may be more variable than that based on numbers because large animals (which are the major contributors to the resulting statistic) are rare and poorly sampled with a grab. This variability makes interpretation of data or statistical assessment of trends or gradients in biomass diversity much more difficult than with diversity based on numbers.

The usual practice in benthic studies has been to work only with a single taxon (Rex, 1973) or preferably several numerically dominant taxa, such as polychaetes and bivalves (Hessler and Sanders, 1967; Sanders, 1968; and Slobodkin and Sanders, 1969). This practice ignores the entire assemblage of organisms which are interacting with polychaetes and bivalves. In this study all invertebrate organisms contained in the grab sample and retained on 0.42 mm-mesh screen were used in the analysis. Indubitably only a small percentage

of nematodes present in the sediment were retained on the screen. However, those retained contribute to the energetics of the assemblage and then unknown in community structure analyses eliminates the bias which results from considering only one or two taxa. Oligochaetes, since they were not sorted to species, were excluded in species-diversity calculations. This allowed a description of an almost entire assemblage of animals, composing a major portion of the biomass in the sediments. To facilitate comparison to other works diversity values calculated without nematodes (which were numerically important in this study) are presented in Appendix IV.

Latitudinal gradients in species diversity have been recognized for some time and several hypotheses have been advanced to explain the phenomenon (Pianka, 1966). The time-growth theory states that all communities tend to diversify with time. The theory of spatial heterogeneity is that the more complex the physical environment the more complex and diverse the flora and fauna (Simpson, 1964). Latitudinal gradients have also been suggested to result from a change from physical to biologically controlled environments (Dobzhansky, 1950). The theory of climatic stability is that diversity is high in areas with constant resources and climates (Connell and Orias, 1964). Each or a combination of these theories may apply in various situations.

Diversity in the deep sea is generally explained by Sanders' (1968) Stability-Time hypothesis. This hypothesis states that over geologic time (millions of years) an environment with low physical stress will develop a highly diverse community. As the stress gradient increases the community changes to one of low diversity. Communities are thought to range along an environmental continuum in which interspecific competition plays an increasingly important role as physical stress decreases.

A parallel concept is the r - K continuum of Pianka (1971). Organisms typically occurring in regions of environmental stress tend to have high reproductive rates and rapid development. MacArthur and Wilson (1967) have referred to such organisms as r - selected. K - selected organisms produce fewer off-spring and have a long development period. At the r - end of Pianka's continuum no competition for energy sources exists, optimal strategy is to put the majority of energy into reproduction, leading to high productivity. At the K - end of the spectrum competition is strong and energy is used for maintenance and the support of a few young.

Primary influence on diversity can be a factor other than the physical environment. Dayton (1971) showed that even in physically stressed (rocky intertidal) environments the community structure was influenced by competition

and predation. In an antarctic sponge community predation was the primary factor influencing community organization (Dayton, Robilliard, Paine, and Dayont, 1974). Woodin (1974) found that biological interactions were of paramount importance to the determination of community structure in a soft sediment environment.

In the above works natural predators have been shown, by experiments, to inhibit competitive exclusion in intertidal (Dayton, 1971) and subtidal environments (Woodin, 1974). This elimination of predators caused diversity to decrease. These results have been extended to an hypothesis that deep-sea diversity is high because competitive exclusion is prevented by "croppers" or large species which are non-selective in their feeding habits (Dayton and Hessler, 1972). Grassle and Sanders (1973) argued that observed life history strategies of deep-sea species would not be selected for by such a mechanism, and therefore could be of only minor significance.

Little work has been done on the causative relationship between community function and its structural parameters. Smith, Rowe, and Nichols (1973) found that in an area of high organic carbon (sewage effluent) and seemingly adequate dissolved oxgyen (4 ml/l), the benthic community was structured with small r-selected species (mostly nematodes), for rapid utilization of the available excess organic material. Sediment characteristics and their effect on

community structure have been examined by Rhoads and Young (1970) and Young and Rhoads (1971), who have shown that filter-feeding organisms are excluded from communities in areas where surface sediment is easily resuspended by low-velocity currents. They suggested that sediment re-working by deposit feeding organisms creates such conditions. Wieser (1959) has shown the importance of grain size in regulating the structure of interstitial communities.

Theede, Ponat, Hiroki and Schlieper (1969) found that some marine invertebrates were able to survive in oxygen-deficient and H_2S containing environments. Experiments with isolated gill tissue indicated that adaption to oxygen-deficiency had occurred on the cellular level. Grassle and Grassle (1974) followed repopulation of marine benthic organisms after an oil spill. Initially, the polychaete Capitella capitata increased most rapidly in numerical abundance and then sharply declined. Such behaviour is indicative of an opportunistic species. Electrophoretic studies of the opportunistic C. capitata showed that single genotypes were present at each loci. C. capitata populations in undisturbed environments were small in number and several genotypes were present. Thus, adaption to a disturbed environment has been shown to occur on a molecular level.

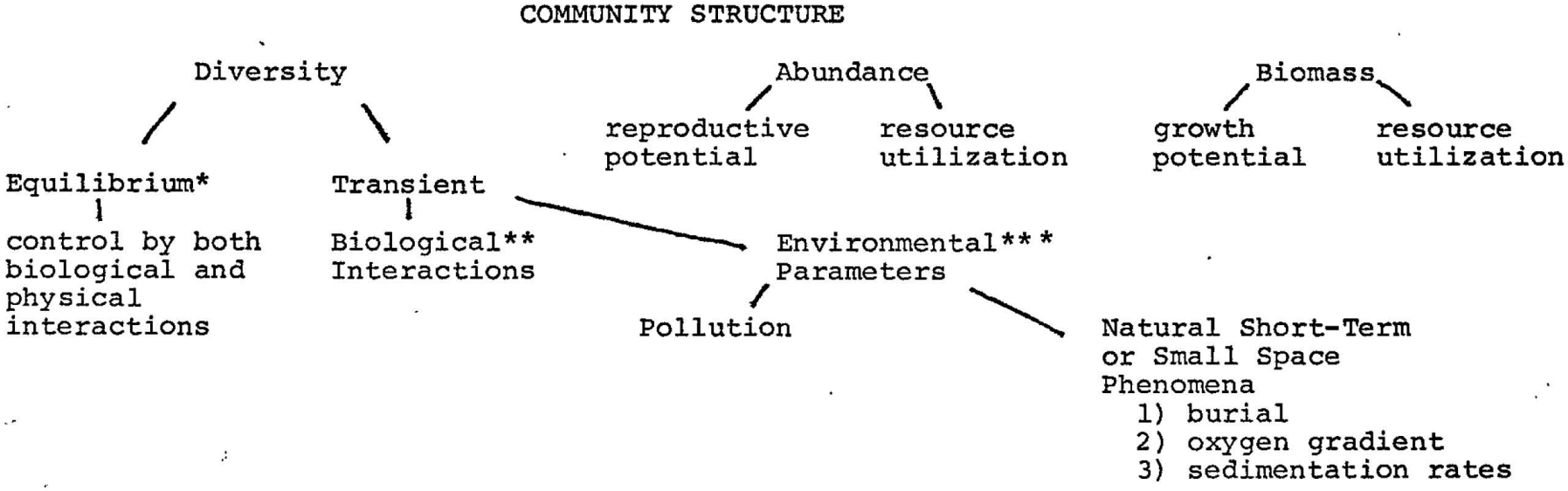
Statement of Problem

The stability-time hypothesis considers epochs of geologic time. During thousands of years of environmental stability communities are able to evolve into highly diverse assemblages. However, within a geologic time period the assemblage may be exposed to many short-term fluctuations that cause variations on a much smaller time scale.

The smaller time scale, ecological time, has two components: 1) generation time of the organisms and 2) the longevity of the community. In these shorter time-scales, influences on community structure are through biological and physical factors acting directly on the individual organisms. Factors such as larval recruitment, predation, and changes in the physical environment operate during both generation time and community lifespan.

Grassle and Sanders (1973) have proposed that short-term fluctuations in the environment result in communities which are characterized by a "transient diversity" as opposed to an equilibrium diversity. As environmental records have not been taken over geologic epochs, it is difficult to differentiate between transient and equilibrium diversity. Thus it must be assumed that any community structure is the sum of both transient and equilibrium components.

Figure 1. Schematic representation of community structure components.



* Structure controlled by long-term physical phenomena

** Structure controlled by K-regulated species

*** Structure controlled by short-term or mesoscale space phenomena

Transient structure can be the product of biological factors such as predation, competition, crowding, etc. as reviewed in the Introduction. But transient structure can also be the result of physical or chemical environmental parameters. (See figure I.) Most recent attention has been focused on pollution stress, but physical conditions important to transient community structure can have natural origins as well. In the oceans the origin could be circulation, seasonable variability, salinity, oxygen, and for the bottom, the conditions of the sediments.

This study is an examination of the effects of natural short-term fluctuations or gradients in the physical-chemical milieu on benthic community structure. The structural components to be dealt with are 1) diversity, 2) biomass, and 3) abundance, and their relation to 1) gradients in dissolved-oxygen in the bottom water, 2) catastrophic burial, and 3) high rates of sedimentation.

CHAPTER II

LOW - OXYGEN STRESS

Rhoads and Morse (1971) have reviewed the literature on low-oxygen regions of the Black Sea, Gulf of California and continental borderland basins of California. They concluded that: (1) water containing less than 0.1 ml O_2/l is azoic, (2) oxygen concentrations between 0.3 and 1 ml O_2/l support a low diversity assemblage of small soft-bodied infauna, and (3) as the oxygen concentration exceeds 1.0 ml/l species diversity increases significantly, particularly for calcareous species. They suggested that extended periods of anaerobic respiration may cause dissolution of calcium carbonate tests, thus limiting calcareous organisms to areas with higher oxygen concentrations.

Thus, insufficient oxygen in the environment can have a primary influence on the structure of the benthic community. When available oxygen is low, what types of animals dominate the community? What effect does a variable oxygen supply have on community structure? Golfo Dulce, off the west coast of Costa Rica, and the Fosa de Cariaco, off the north coast of Venezuela, are areas of oxygen depletion from which samples were obtained to answer these questions.

Golfo Dulce

Golfo Dulce is an anoxic basin that intermittently receives oxygen enriching water. As such it provides an opportunity to study invertebrate community relationships in a region of intermittent low-oxygen stress. The gulf lies between 8°27' and 8°45'N latitude on the western coast of Costa Rica (Figure 2). It is approximately 20 km in length, has a sill depth of 64 meters, and a maximum depth of 200 m. Richards, Anderson and Cline (1971) have recorded hydrogen sulphide concentrations of 5 ug-atoms/liter in the bottom water of the basin. The basin receives boluses of new water at intermittent intervals. Richards et al. postulated that internal wave activity and coastal upwelling combine to introduce, at the sill, water denser than that at intermediate depths in the basin. The water flows north towards the head of the gulf, sinking as it progresses and enriching the oxygen content of the bottom water.

Fosa de Cariaco

The Fosa de Cariaco is a basin about 192 km long and 59 km wide with a sill depth of 150 meters (Figure 3). It trends in an east-west direction and is composed of

Figure 2. Golfo Dulce, Costa Rica. Approximate bathymetry, station locations, and bottom water oxygen concentrations. From H.O. 21562.

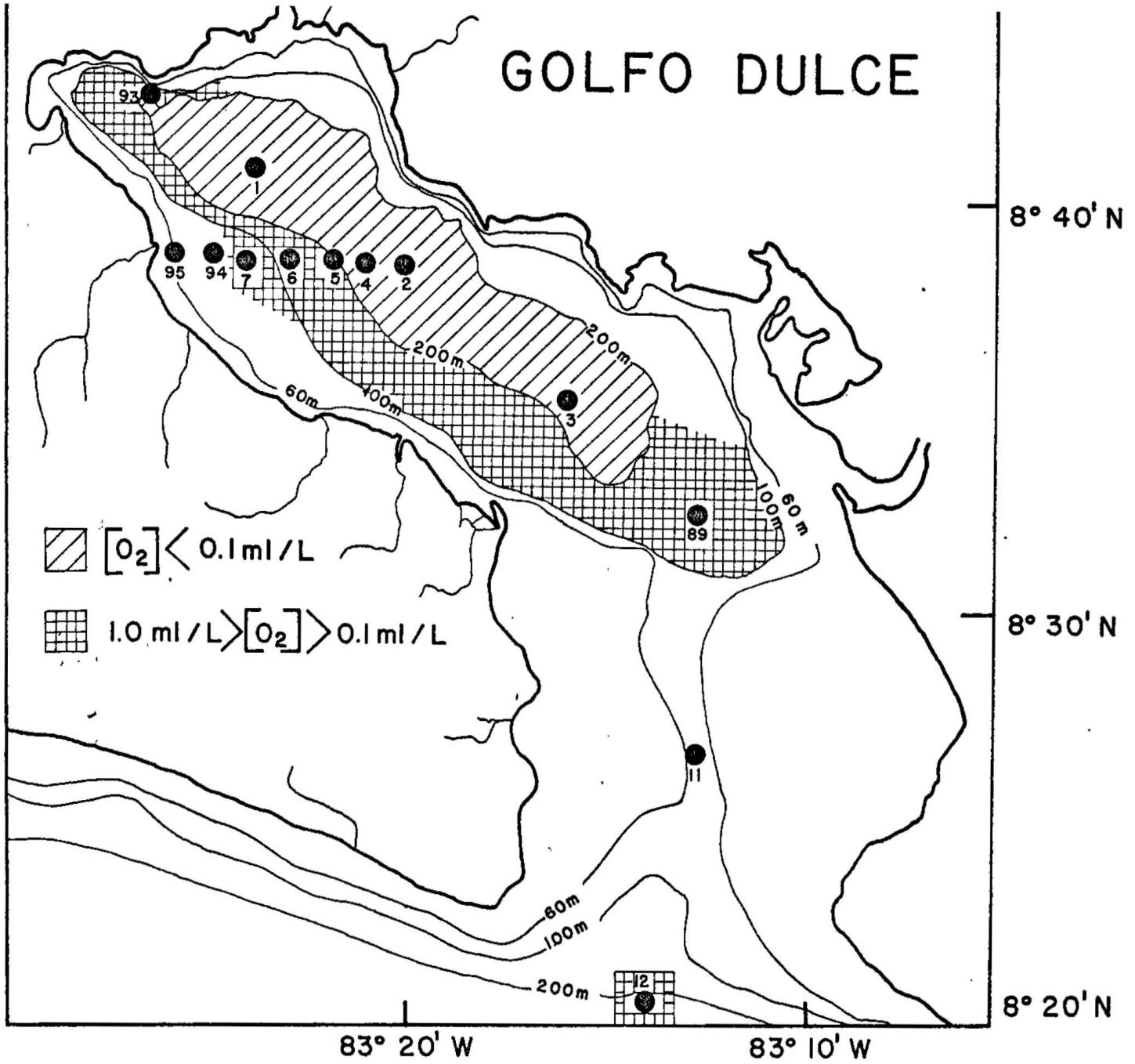

GOLFO DULCE
93
1
95
94
7
6
5
4
2
3
89
11
12
200m
100m
60m
$[O_2] < 0.1$ ml/L
1.0 ml/L $> [O_2] >$ 0.1 ml/L
8° 40' N
8° 30' N
8° 20' N
83° 20' W
83° 10' W

Figure 3. Chart of the Fosa de Cariaco showing station locations and depth. Prepared from charts BC 0703 N and HO 6573.

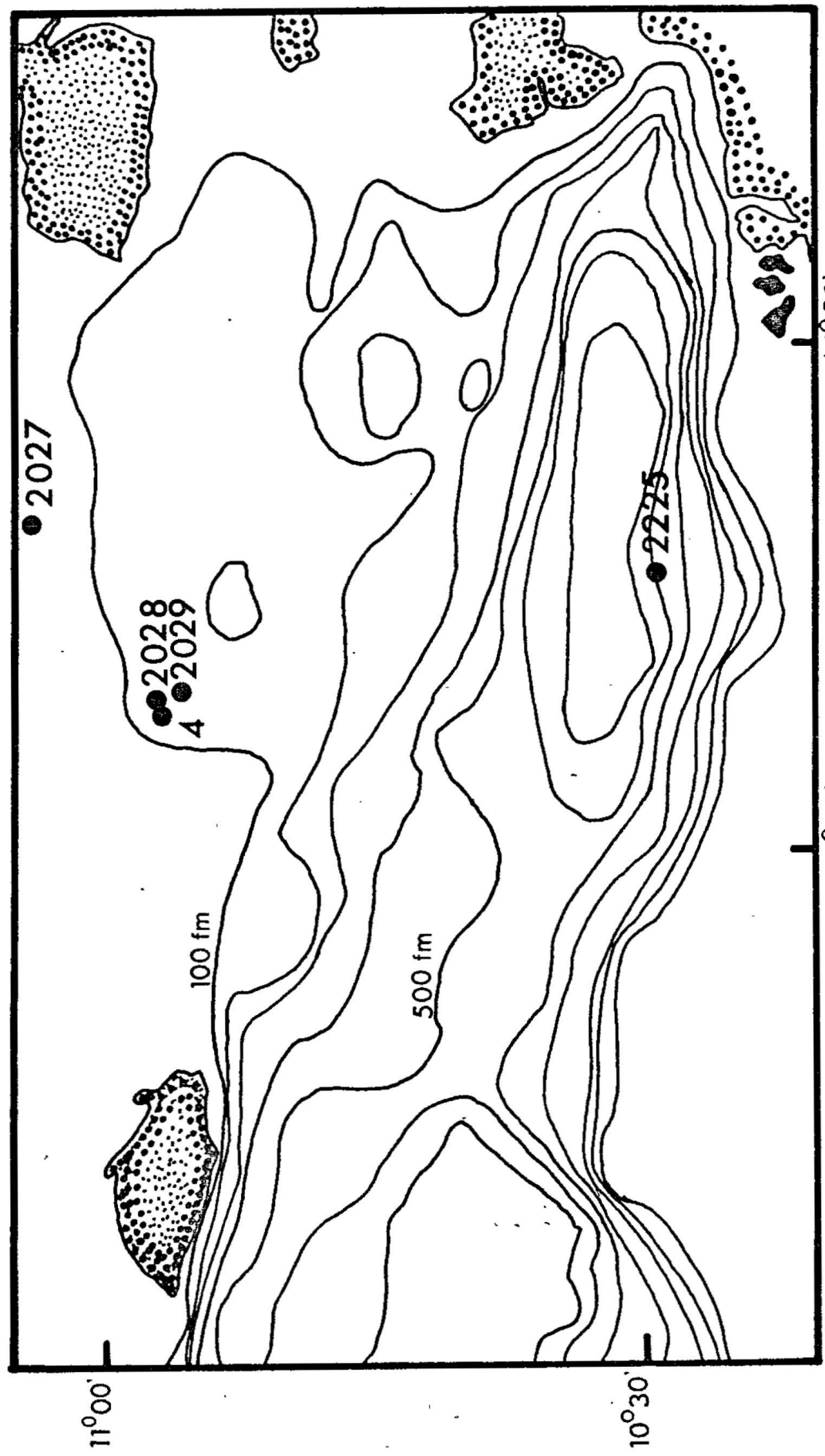


Figure 3

two deeps approximately 1400 m in depth separated by a sill 900 m deep. In 1954 L. V. Worthington discovered that the waters below 400 meters in the basin were anoxic and had a distinct odor of hydrogen sulfide. Richards and Vaccaro (1956) found anoxic waters below 375 meters and hydrogen sulfide in concentrations ranging up to 0.03 mg-a sulfide sulfur per liter. Since then the geology, hydrography, chemistry and plankton of the area have been the subject of several studies (Lidz et al., 1969; Curl, 1960; Zoppi, 1961; Legare, 1961), but little work has been done on the benthos of the area.

Heezen, Menzies, Broecker and Ewing (1959) place the start of stagnation about 11,000 B.P., or about the end of the last glacial period. It has been suggested that the warming that occurred at that time and the shallow sill depth combined to produce the stagnant waters (Heezen et al., 1959; Worthington, personal communication).

Richards and Vaccaro (1956) found that the temperature in the Fosa decreased steadily from surface values of 24° -- 26°C to about 18°C just below sill depth. At 460 m the temperature was 17°C and remained at this value to the bottom. Salinity ranged from 35-36‰ at the surface, by 500 m it was about 36.2‰ and remained at this value to

the bottom. Outside the basin both temperature and salinity were similar to that in the basin above sill depth. Below sill depth they continued to decrease falling to 8.60°C and 34.91‰ at 488 m. The distribution of temperature and salinity, thus, shows the isolation of basin waters below sill depth.

METHODS

All samples from the Golfo Dulce were obtained during Cruise 76 of R/V T. G. Thompson. Fosa de Cariaco samples were obtained on R/V Atlantis II Cruise 79 and Cruise 86. Two bottom grab samples were obtained with a 0.1 m^2 van Veen grab at thirteen stations in Golfo Dulce. A 0.2 m^2 van Veen grab was used to obtain five samples in the Fosa de Cariaco on AII Cruise 79. A 0.1 m^2 van Veen grab was used on AII Cruise 86 to obtain five samples. On board ship the samples were sieved through a 0.42-mm-mesh screen and fixed with 10% formalin in seawater buffered with borax. Upon return to the laboratory the TGT 76 and AII 79 samples were again sieved through 0.42-mm-mesh screen and sorted with a dissecting microscope. R/V Atlantic II 86 samples were sorted on board ship. After sorting, the animals were stored in 80% alcohol. Animals were identified to species; fragments of polychaetes were identified to family. Wet weights of the preserved animals were obtained

by blotting each animal on a paper towel for three minutes and then weighing on a Mettler microbalance. Organic carbon and nitrogen content of Golfo Dulce sediments was determined with a Perkin Elmer Elemental Analyzer, after acid removal of calcium carbonate. Oxygen content of bottom water was determined by Winkler titration. The concentration of thiosulfate, which influences the volume used, controls the lower limit of the assay. In this study 0.05 ml 0_2/l $\pm$ 0.02-0.05 m/0_2/l was considered the lower limit (Carrit and Carpenter, 1966).

Species diversity was determined with the Shannon-Wiener Information Function as previous described in Chapter I. Species diversity indices respond to two factors, the number of species present (or species richness) and the distribution of individuals among the species. Evenness of distribution within a sample (E/S) was determined by the ratio of the number of hypothetical "equitable distributed" species (e^H) to the actual number of observed species (Pielou, 1966; Buzas and Gibson, 1969). An equally apportioned sample would have an E/S value = 1; lower values indicate less equal distribution of species, hence greater dominance by a few, within the sample (Sanders, 1968). It has been suggested that evenness indices are not valid because of sensitivity to changes in number of species (Peet, 1974). However, when used in conjunction with diversity measurements they indicate which component of the diversity measurement is of greatest importance.

RESULTS

Golfo Dulce

Oxygen content of sill bottom water was 1.65 ml/l; below sill depth, 64 m, bottom water oxygen content was less than 1 ml/l. In the deepest section of the basin (200 m) the bottom water oxygen decreased from 0.07 ml/l at station 3 to undetectable amounts at station 1. Outside the basin (station 12) bottom water contained 0.63 ml O_2/l (see Figure 2).

Table 1 lists the percent organic content of the surface sediments. Carbon content was around 2% by weight throughout the basin. Carbon/nitrogen ratio was highest (10) at the sill; both carbon and nitrogen contents were lower (0.36 and 0.04 percent respectively) than at any other station in the gulf. Many factors influence C/N ratios (Bader, 1955) making it impossible to determine the meaning of the low ratios found in Golfo Dulce. However, there was no correlation between animal distribution and organic content of the surface sediments.

Bottom photographs show the sill to have little slope, but with well developed ripple marks and scouring around rocks. Urchins appear in sill photos along with several light-colored vermiform organisms. Photographs taken at station 6 show large leaves and coconuts on a flat mud bottom with no evidence of animal life. At station 89 the bottom water was murky; however, a flat and probably azoic bottom was discernible.

Table 1

Percent Organic Content of Surface Sediment by Weight

(Golfo Dulce)

Station No.	Depth (m)	N (%)	C (%)	H (%)	C/N
1	192	0.28	1.80	1.11	6.5
2	182	0.22	2.14	0.96	9.7
3	190	0.27	2.17	1.12	8.2
7	70	0.40	2.05	1.04	5.2
11	70	0.04	0.36	0.40	9.0
89	134	0.18	1.58	1.06	8.8

Live animals were found in grab samples at all stations within the basin shallower than 100 m. (A complete species list is contained in Appendix I.) At depths greater than 100 m the samples were either azoic or contained one or two individuals of the amphipod genus Erichthonius (Table 2). This amphipod is probably a contaminant from the ship's hull introduced through the seawater system. Samples from station 7 (70 m) contained a total of twenty-seven polychaete species. Paraonis lyra was the numerically dominant species in both samples. The decapods, Betaus sp. and Carcinoplacinid Pilumnoplax americana composed the dominant portion of the total biomass at the station. At station 11, located on the sill, samples contained specimens representing eleven orders. A caprellid amphipod, (cf.) Petrotripus brevis was the numerically-dominant species in both samples. Vertebrates and hemi-chordates were represented by single individuals of Conger congus and Phoronis sp. Polychaetes were represented by twenty-five species, amphipods by six species, pelecypods by two and nemerteans and nematodes each one had representative. At the same depth within the embayment, station 95, there were seven polychaetes, two pelecypods, two amphipods, and one cumacean species represented. The numerically dominant species in sample A was the polychaete Paraonis lyra. In sample B numerical dominance was shared by three species of polychaetes, a spinonid, the pilargid Sigambra tentaculata,

Table 2

Number of species, individuals, and total biomass for each grab sample (Golfo Dulce)

Sample No.	No. of species	No. of individuals	Total biomass (mg)
1 a&b	0	0	0.0
2 a&b	0	0	0.0
3 a	1	2	5.9
3 b	1	1	1.3
4 a&b	0	0	0.0
5 a	1	2	11.3
5 b	0	0	0.0
6 a&b	0	0	0.0
7 a	24	924	789.5
7 b	15	348	1,707.2
11 a	29	140	4,638.4
11 b	18	65	113.8
12 a	7	13	31.2
12 b	2	2	2.4
89 a	0	0	0.0
89 b	1	1	0.1
93 a&b	0	0	0.0
94 a	0	0	0.0
94 b	1	1	0.4
95 a	8	32	137.4
95 b	7	15	111.3

and lumbrinereid Ninoe sp. Amphipods were represented by single individuals of the species Corophium bonelli and Erichthonius sp. Bivalves Nucula scheneki and Adrana sp. were also represented by a single specimen. The cumacean Eudorella sp. was represented by two individuals. There were eight species outside the basin at station twelve (200 m). Nematodes, represented by four individuals, were numerically dominant. The polychaete Pareulepis sp. contributed the largest amount of biomass with a single individual of 12.2 mg. The amphipod Erichthonius sp. was again represented by one individual as was the cumacean Eudorella sp.

Table 3 contains diversity (H(s)) and evenness (E/S) values for all samples containing more than one species. Both infauna and epifauna are included as the distinction between these catagories is at best artificial and vague for a sediment bottom. It does not include the eel Congers congrus.

Diversity values within the basin fell into the narrow range of 1.3 to 1.8. These values are low based on what would be expected from published data on marine benthos (Sanders, 1968), as are the values from the one station outside the basin. Values of 2.843 and 2.401 for the sill station are low for a nonstressed tropical environment, but this may be a function of the small sample size.

Evenness values are greater than 0.5 outside of the basin and at stations within the basin at sill depth.

Table 3

Diversity (H(s)) and evenness (E/S) based on numbers of species and biomass of species for all samples containing more than one species. (Golfo Dulce).

Sample No.	Numbers		Biomass	
	H(s)	E/S	H(s)	E/S
7 a	1.599	0.202	1.033	0.117
7 b	1.624	0.317	1.067	0.182
11 a	2.877	0.634	1.352	0.138
11 b	2.401	0.613	2.178	0.491
12 a	1.778	0.846	1.494	0.495
12 b	0.693	1.000	0.677	0.984
95 a	1.377	0 495	1.035	0.352
95 b	1.807	0.870	1.156	0.454

Stations below sill depth have values of 0.3 or lower. This trend is more pronounced in evenness calculations based on biomass.

The values of evenness are dependent on sample size. When the number of species present is small, the reliability that the sample is representative of the area is lessened. Evenness fluctuations were tested by calculations with hypothetical numbers of species and the e^H value for the sample. At the sill station a change of two in the number of species present caused a 0.1 change in the evenness value. At station 7, within the basin, a change of four species resulted in a 0.04 change in evenness. Though the numbers are small, the sampling procedure provided adequate material. Thus, the calculated evenness values are considered reliable indices of the importance of the distribution of individuals among the species.

Another parameter that describes a community is the distribution of biomass. At all stations within the basin (with more than one species present) and the sill station, the average individual biomass of the numerically dominant species was within the range 0.12-0.17 mg/ind. At station 12, outside the basin, a polychaete Glycinde armigera, was the numerically dominant species and had an average individual biomass of 1.3 mg. A few individuals representing larger species occurred at all stations. However at stations where the bottom-water oxygen content was less than 1 ml/l

dominant individuals were motile species such as the amphipod Ericthonius sp. and the shrimp Betaus sp. Only the sill and station 95 (62 m) samples contained bivalves, which close their shells in an attempt to tolerate periods of low oxygen stress (Jackson, 1972).

Fosa de Cariaco

Station locations in the Fosa de Cariaco are shown in Figure 3. Temperature, salinity, and oxygen profiles of the water column at AII 79 stations, and AII 86 station 2225 (Figures 4-6) indicate that the same water mass overlies the trench with anoxic conditions developing at about 300 m depth. At station 2027 (Cruise 76) the bottom water oxygen content was 3.16 ml/l, one grab sample was taken. This sample contained 341 individuals representing 75 species. (See appendix II for complete species listing. Nematodes are sorted to species.) Numerically the polychaete Nephtys squamosa dominated the sample while a Goneplacidae decapod provided the majority of the 4.39 g biomass.

Two grab samples were obtained at station 2028 and 2029 (Cruise 76). Bottom water dissolved oxygen was 0.267 ml/l at station 2028. Twenty species and 142 individuals were contained in sample a, while 37 species and 274 individuals

were found in sample b. Nematodes were the numerically dominant group. The nematode Filoncholaimus composed over fifty percent of the nematode fauna in both samples. The polychaete Aricidae suecica provided the majority of the biomass in sample a while a Pagurinae crab dominated sample b. Total biomass was respectively .018 g and 0.223 g. In both samples a bivalve was numerically important; however these animals were quite small and possibly represent a recent set. At station 2029 the bottom water was anoxic; one sample contained two species of nematoda each represented by one individual. The second sample was azoic.

At Station 4 (AII 86) five meters above the bottom dissolved-oxygen was 0.73 ml/l. This value falls on the oxygen-depth curve for Station 2225, which is further evidence for homogeneity of the water in the Fosa. Station 4, at a depth of 210 meters, had a bottom water dissolved-oxygen concentration of 0.5 ml/l as indicated by the oxygen profile for the eastern basin of the Fosa.

Five 0.1 m^2 van Veen grab samples were taken at this station. Nematodes were numerically dominant in four samples, with oligochaetes the second most dominant group. In the fifth sample oligochaetes were first and nematodes

second in numerical dominance. Total number of individuals in each sample ranged from 116 to 305. A total of 36 species were represented and the number of species in an individual sample ranged from 13 to 24. A polychaete of the family Chaetopteridae dominated the biomass in samples 2 and 5 and was the second dominant species in sample 6. Bivalves dominated the biomass in the remaining samples. Total biomass ranged between .075 g and .228 g.

Diversity and evenness values for the samples containing animals are given in Table 4 (Oligochaetes were not included in diversity calculations). At station 2027 the diversity value 3.729 is an expected value for a tropical sample. Values at station 2028 are similar to those found at the sill station of Golfo Dulce and are high for a stressed area. Evenness values are greater than 0.5 for the two 0.2 m^2 samples with diversity values greater than 2.8. A lower diversity value is accompanied by a lower evenness value in sample 2028 a. Samples from Atlantis II station 4 cannot be directly compared to those from station 2027 and 2028 because of the smaller sample size. However, diversity values range between 1.927 and 2.429 which is also high for a stressed area. All samples followed the pattern of greater diversity being associated with greater evenness when species list length was similar.

Figure 4. Temperature profiles for stations in Fosa de Cariaco.

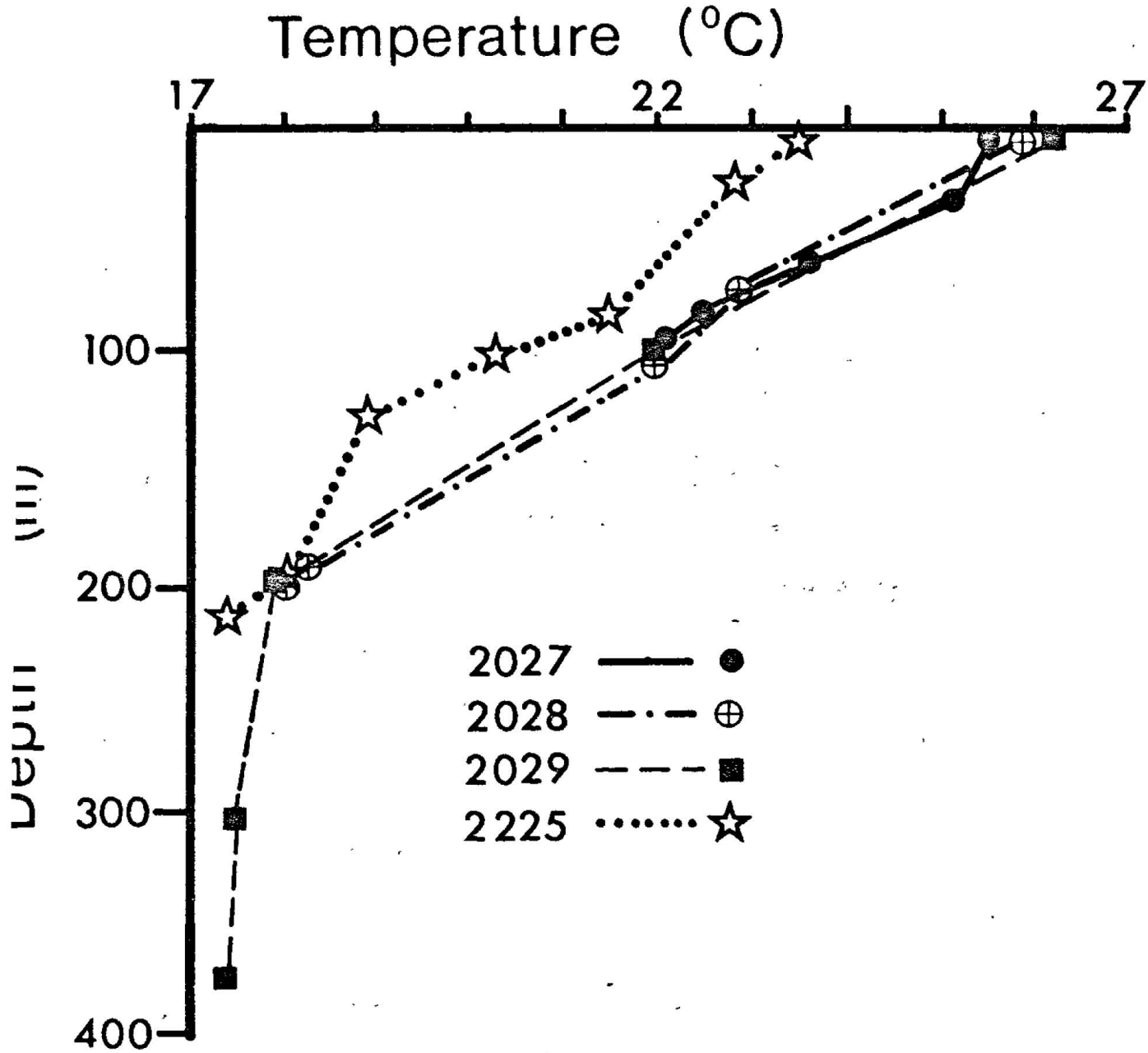

Temperature (°C)
17
22
27
100
200
300
400
Depth (m)
2027
2028
2029
2225

Figure 4

Figure 5. Salinity profile for stations in Fosa de Cariaco.

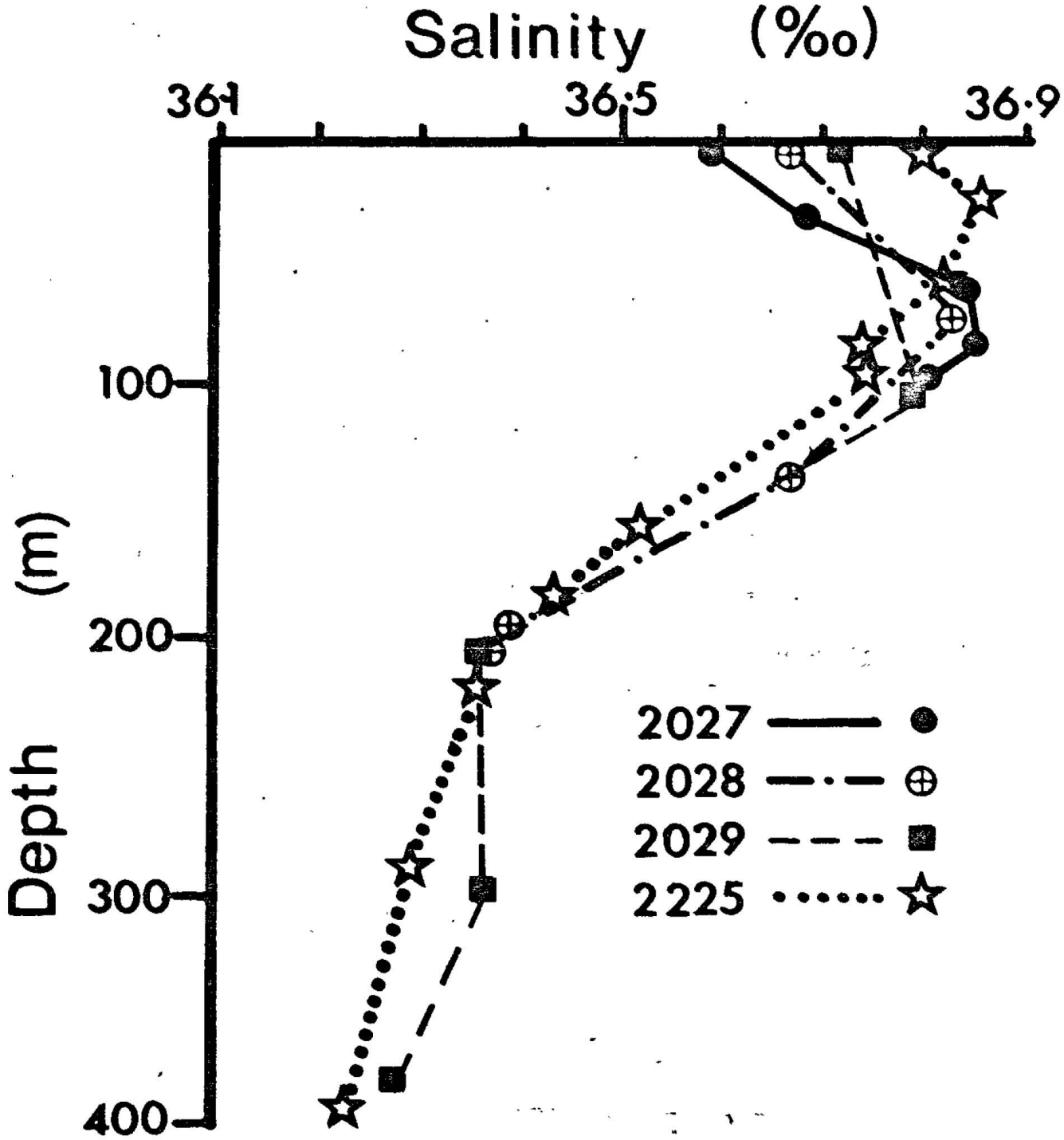

Salinity (‰)
36·1
36·5
36·9
100
200
300
400
Depth (m)
2027
2028
2029
2225

Figure 5

Figure 6. Oxygen profile for stations in the Fosa de Cariaco.

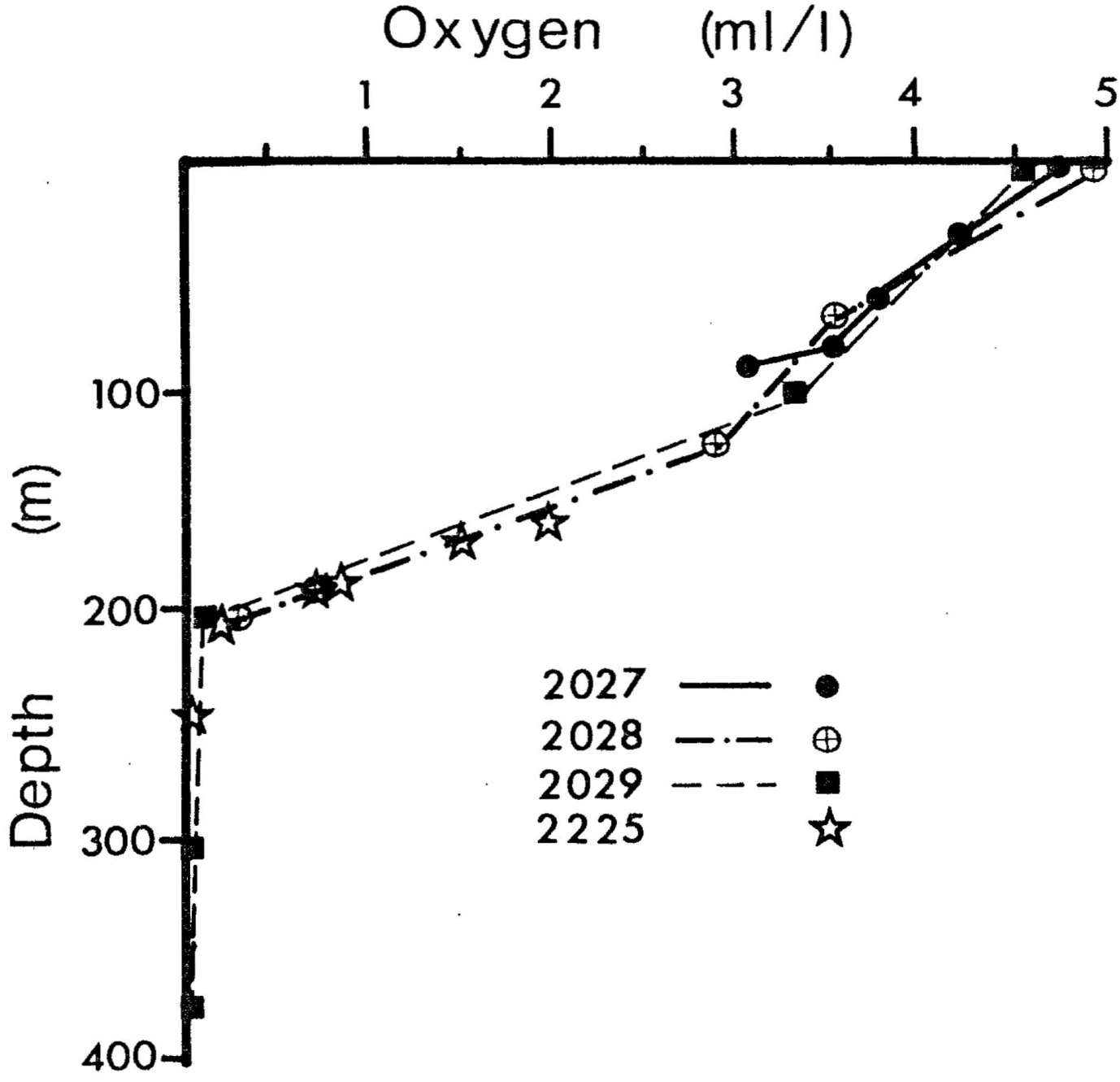


Figure 6

Table 4

Diversity and Evenness Values for Fosa de Cariaco

(Based on numbers)*

	Station No.	Depth (m)	H'(s)	E/S
	2027	90	3.729	0.555
0.2 m^2 grab	2028a	202	1.618	0.280
	2028b	202	2.883	0.510
	4-2	210	1.927	0.528
	4-4	210	2.357	0.480
0.1 m^2 grab	4-5	210	2.366	0.484
	4-6	210	1.953	0.504
	4-7	210	2.429	0.473

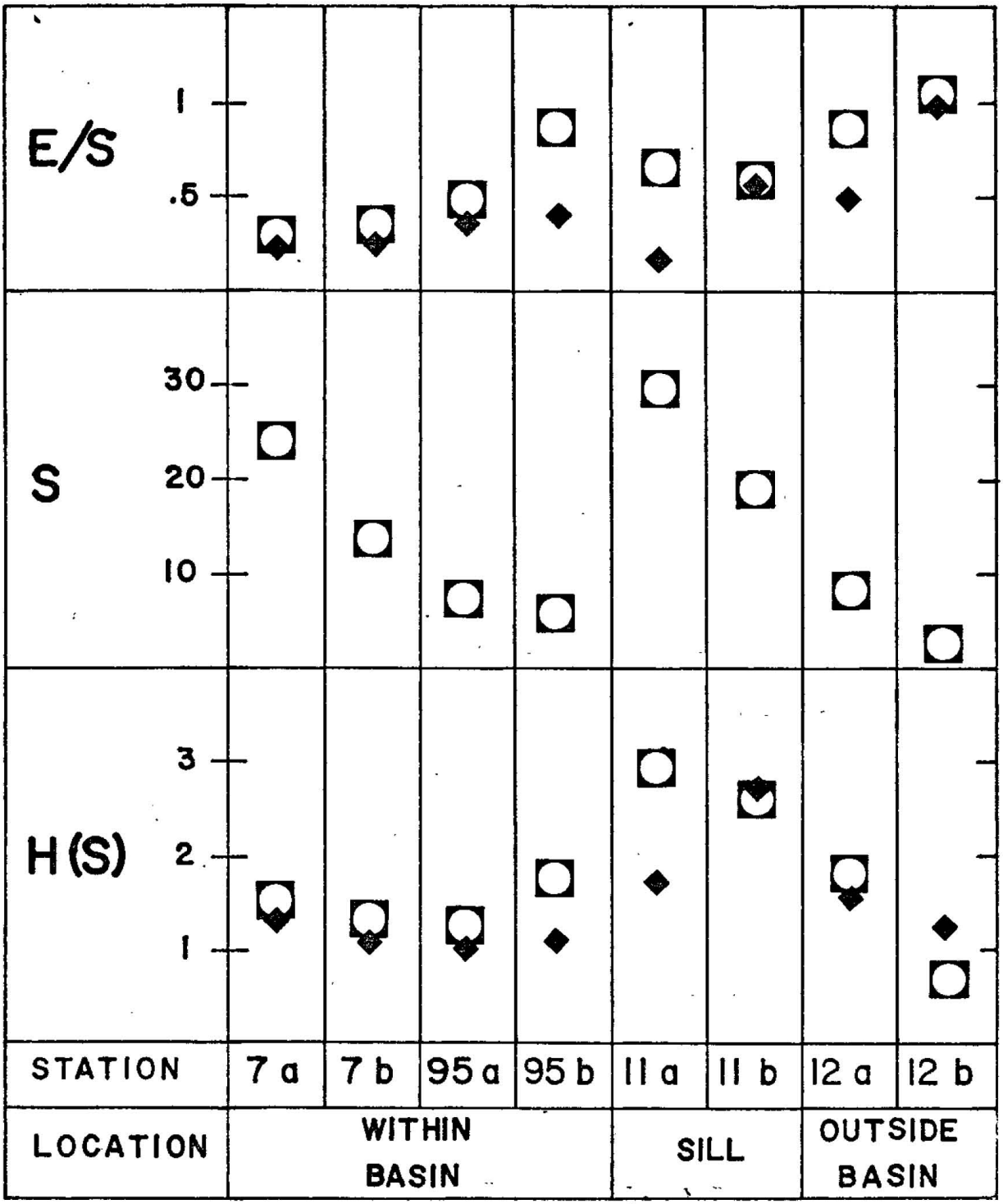
* Species lists on which these statistics are based can be found in App. 2. These values were calculated excluding Oligochaetes, as they were not separated to species.

DISCUSSION

The measurement of H'(s) responded to both the number of species, and the distribution of individuals among species. In general higher values of H'(s) occurred when the species present were equally represented. Inside the Gulfo at the deepest station with animals (Figure 7, Station 7) number of species was relatively high but diversity was not because the species were so numerically dominated by Paraonis lyra. The evenness there was lowest for all stations. In contrast to this, outside the basin (Station 12) there were fewer species than at any other station, but H'(s) was equivalent to Station 7 and 95 because the species were more equitably distributed. Evenness there was highest among all the stations. Diversity values based on biomass of sample 11a also showed a greater dependence upon evenness of distribution than number of species. The significance of H'(s) having greater dependence upon E/S rather than S is not well understood (Buzas and Gibson, 1969). However, the data suggest that the communities were more evenly structured when oxygen availability is more predictable. Even distribution might permit more paths of resource utilization than are available to communities in the basin with a variable oxygen supply.

Further support of these data comes from the organisms, living and dead, found at station 7. Large numbers (4 liters in volume) of empty mollusc shells (most with drill holes), both gastropods and pelecypods, living shrimps, and

Figure 7. Diversity (H(s)), evenness (E/S), and the number of species (s) for samples from Golfo Dulce. Circles are values calculated with number of individuals per species, triangles are values calculated with biomass of species.



E/S = EVENNESS S = NO. OF SPECIES H(S)= DIVERSITY

□ CALCULATED ON BASIS OF NUMBER OF INDIVIDUALS

◆ CALCULATED ON BASIS OF BIOMASS OF SPECIES

Figure 7

carcinoplacinid crabs were found in both samples. The slope of the bottom is not steep in the region of this particular station, so it is unlikely that the shells were transported down slope from another area. A more plausible explanation is that the mollusc shells and decapods are remains of a previous community that existed when the oxygen concentration was higher. As the oxygen supply decreased various components of the community migrated or died until a few species, capable of existing in the stressed environment, dominated the existing community.

The small number of species per sample makes definite conclusions difficult, but it appears that the intermittent flushing occurring in Golfo Dulce causes a fluctuating oxygen concentration that is the primary physical factor controlling the benthos community structure. The result is a community dominated by r-selected species. The numerically dominant species Paraonis lyra is a small (average 0.1 mg/ind.) polychaete. Its distribution is wide-spread even though its small size causes it to be easily missed during sieving and sorting. Paraonidae are known to produce pelagic larvae (Pettibone, 1963) but the life history of P. lyra is not known. Possibly the existence of a pelagic stage allows the polychaete to repeatedly recolonize the stressed region.

The Fosa de Cariaco is not subject to the frequent large fluctuations in bottom water dissolved-oxygen concentration that have been found in Golfo Dulce. Here diversity tended to be greater because of increases in both species richness and evenness of distribution. Biomass tended to be low. This could be because the organisms present did not have the genetic potential for a greater biomass, or the metabolic pathways necessary for growth in the low oxygen region. Pelecypods found in the Fosa had translucent shells, possibly the result of low oxygen concentrations shifting the $HCO_3 \rightleftharpoons CaCO_3$ balance toward HCO_3. However, the presence of organisms such as pelecypods in the low dissolved-oxygen region indicates that with increasingly stable conditions a diverse community composed of several taxa is able to exist.

Futher evidence that stable conditions allow the development of highly diverse communities is seen in the work of Jumars (1974) in the San Diego Trough and Santa Catalina Basin. The San Diego Trough had a constant bottom water dissolved-oxygen concentration of $\sim$0.6-0.7 ml/l, while the concentration in the Santa Catalina Basin was 0.4 ml/l. Using 0.25 m^2 box cores and sieving the samples through a 0.42 mm-mesh screen, Jumars found 318 species in the San Diego Trough and 113 species in Santa Catalina

Basin. The resulting diversity based on rarefaction methods was greater than Sanders, Hessler and Hampson (1965) found on the Gay Head-Bermuda transect. A portion of the greater observed diversity can be attributed to the efficient sampling by the box core (Rowe, et al., in press). However, the large numbers of species representing twelve taxa indicate that stable, on an ecological time scale, stressed-conditions allow the development of a diverse community structure.

Which factors maintain primary control of community structure in stable low-oxygen conditions is not known. As ecological stability develops, more diverse communities might be the result of increased larval recruitment. As more paths of resource utilization develop, abundance of opportunistic species could be controlled by biological factors such as predation and competition for space and available food. It seems probable that the importance of the influence of biological factors on community structure increases as low-oxygen conditions become stable, on an ecological time scale.

Chapter III

SEDIMENTATION STRESS

Benthic organisms must develop life styles which allow them to feed, respire, and reproduce in the presence of sediment. To avoid mechanical damage by sediment particles some organisms have evolved feeding appendages which extend into the water column, others pass sediment through strainers and ingest only food material, while others are capable of passing mineral particles through the gut without damage. Gills may be extended into the water column or protected by tubes or anatomical structures. Strong muscles can develop for moving through the sediment, and larvae may be released into the water column or protected in tubes.

Animal activity results in reworking of the sediment (Rhoads, 1967) and such mechanical movement has been shown to influence faunal composition (Rhoads and Young, 1970). Marshall and Lukas (1970) have shown that the presence of a Zostera marina cover influences the mechanical properties of sediments and the infauna composition. It is presumed that increased turbidity which results from currents carrying unstable sediment can

control faunal composition. Burial, resulting either from turbidity currents, submarine slumping, or man-made dumping may also influence faunal composition. Kranz (1974) has shown that pelecypods are capable of escaping burial by climbing up through the sediment. Saila and Pratt (1972) found, in a laboratory situation, that the polychaete Nephtys incisa was capable of climbing up through 21 cm of mud in less than twenty-four hours. However, it is not known how a typical polychaete - pelecypod mud bottom community responds to burial in the field.

In this study the effects of rapid sedimentation on benthic infaunal communities was studied in two ways: (1) *in situ* burial experiments were carried out in Buzzards Bay to observe the effects of catastrophic burial and (2) collections from an upwelling area off the NW coast of Africa were analyzed to determine the influence of a high bottom-water suspended matter concentrations and high sedimentation rates on the benthic community structure.

IN SITU BURIAL EXPERIMENT

To simulate catastrophic burial an area of bottom sediment at Station K (figure 8) in Buzzards Bay was isolated and buried under controlled amounts of mud.

Figure 8. Chart of Buzzards Bay and Woods Hole Harbor showing location of Station K.

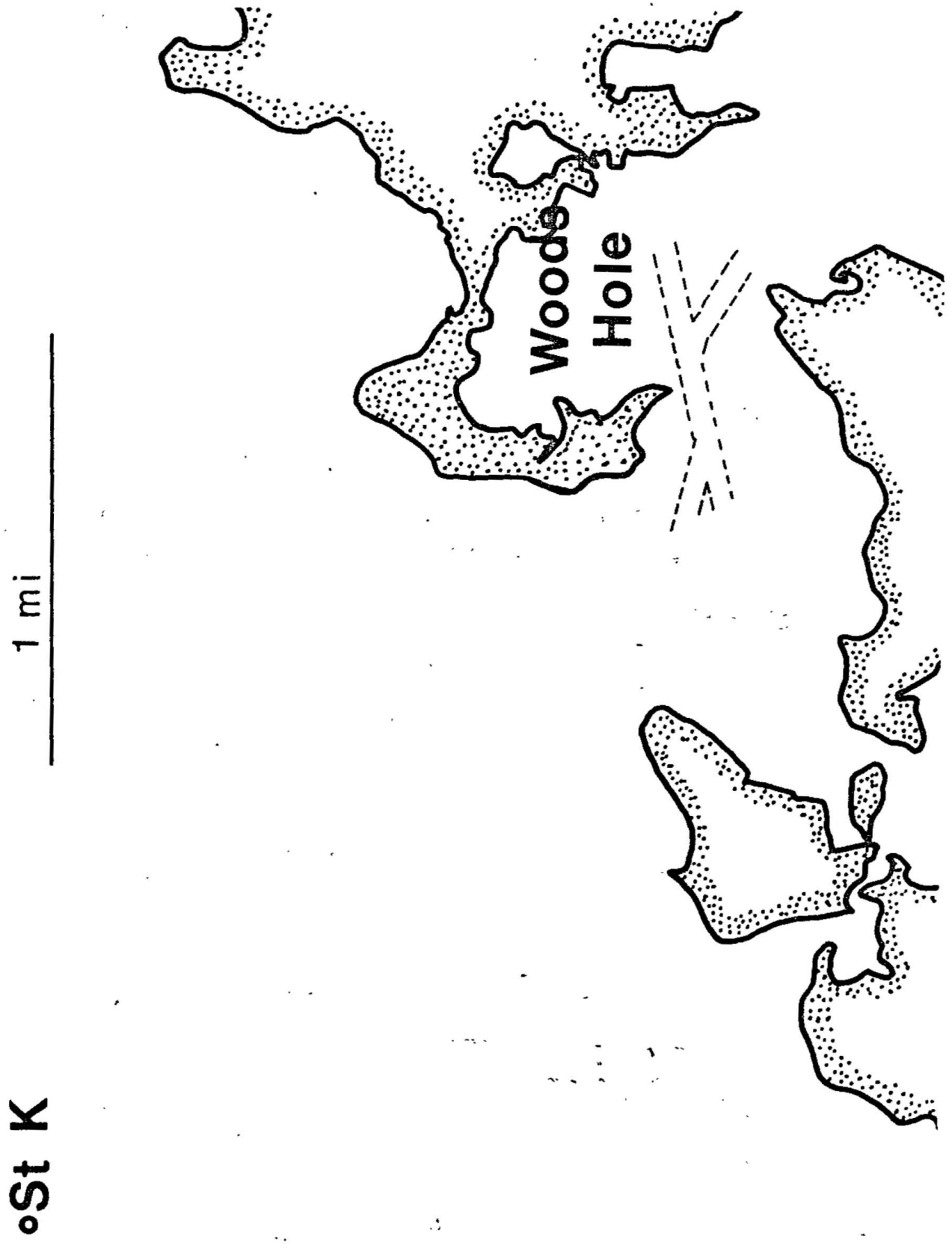


Figure 8

Mud for burial was obtained by sieving native sediment through a 0.297 mm mesh screen and that material which passed through the screen was collected and used for burial. This procedure provided essentially azoic native mud with an organic carbon content of 0.64% and an organic nitrogen content of 0.07% by weight.

Experimental areas to be buried were isolated by one of two methods. In four experiments a plexiglas box 20 cm x 20 cm x 20 cm (figure 9) was filled with the desired amount of burial mud (to a depth of either 5 or 10 cm). SCUBA divers set the box on the study area and removed the top and bottom slides. Retrieval was accomplished by replacing the slides and lifting the box from the sediment. A second diver then took a Birge-Ekman box core, BEBC, sample (Rowe and Clifford, 1973) from the area directly under the box. The second method of isolation used tin cans (15 cm in height, 9.6 cm diameter) with both metal ends removed (figure 9) to contain the sediment and burial mud. Two cans were joined together by wrapping 1/4 inch thick rubber around the joint and securing them with two hose clamps. This procedure allowed several cans to be joined together permitting burial up to 30 cm. The cans were filled with the desired amount of burial mud (5, 10, or 30 cm depth) and capped with

Figure 9. Drawing of plexiglas box and tin cans used in burial experiments.

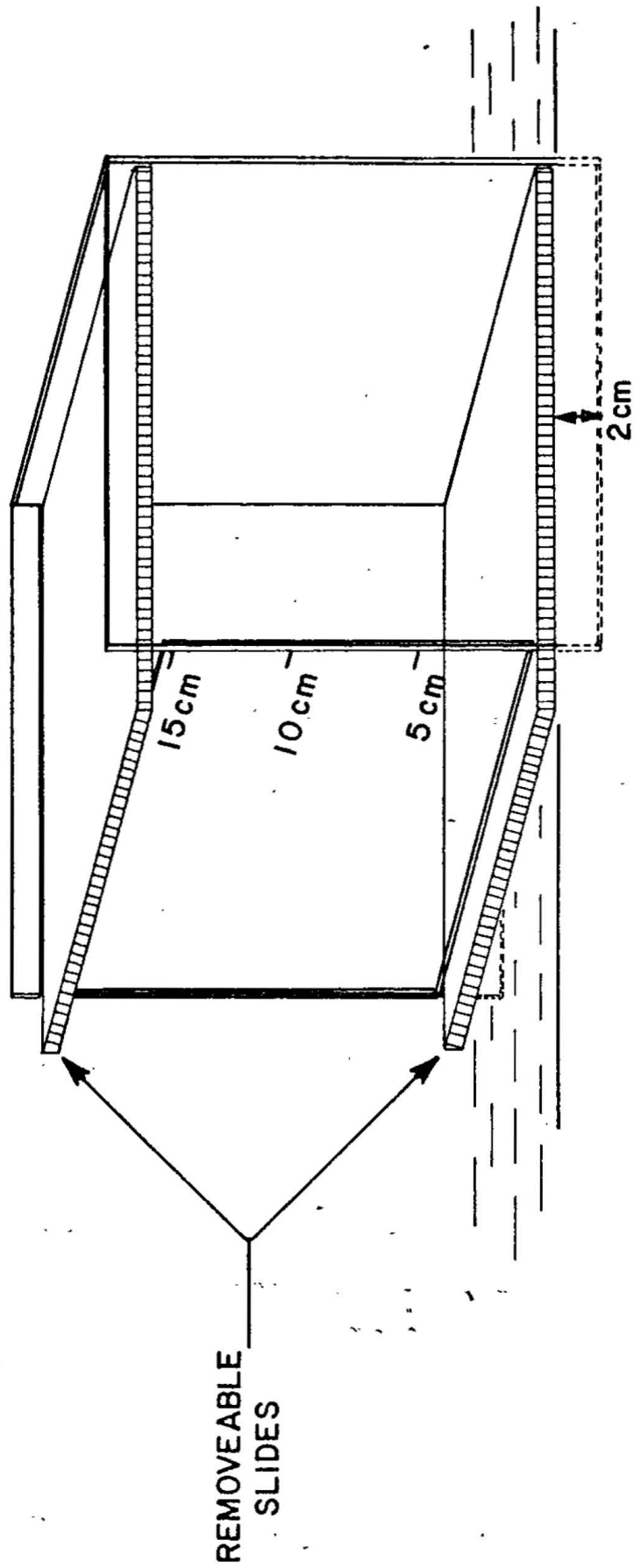
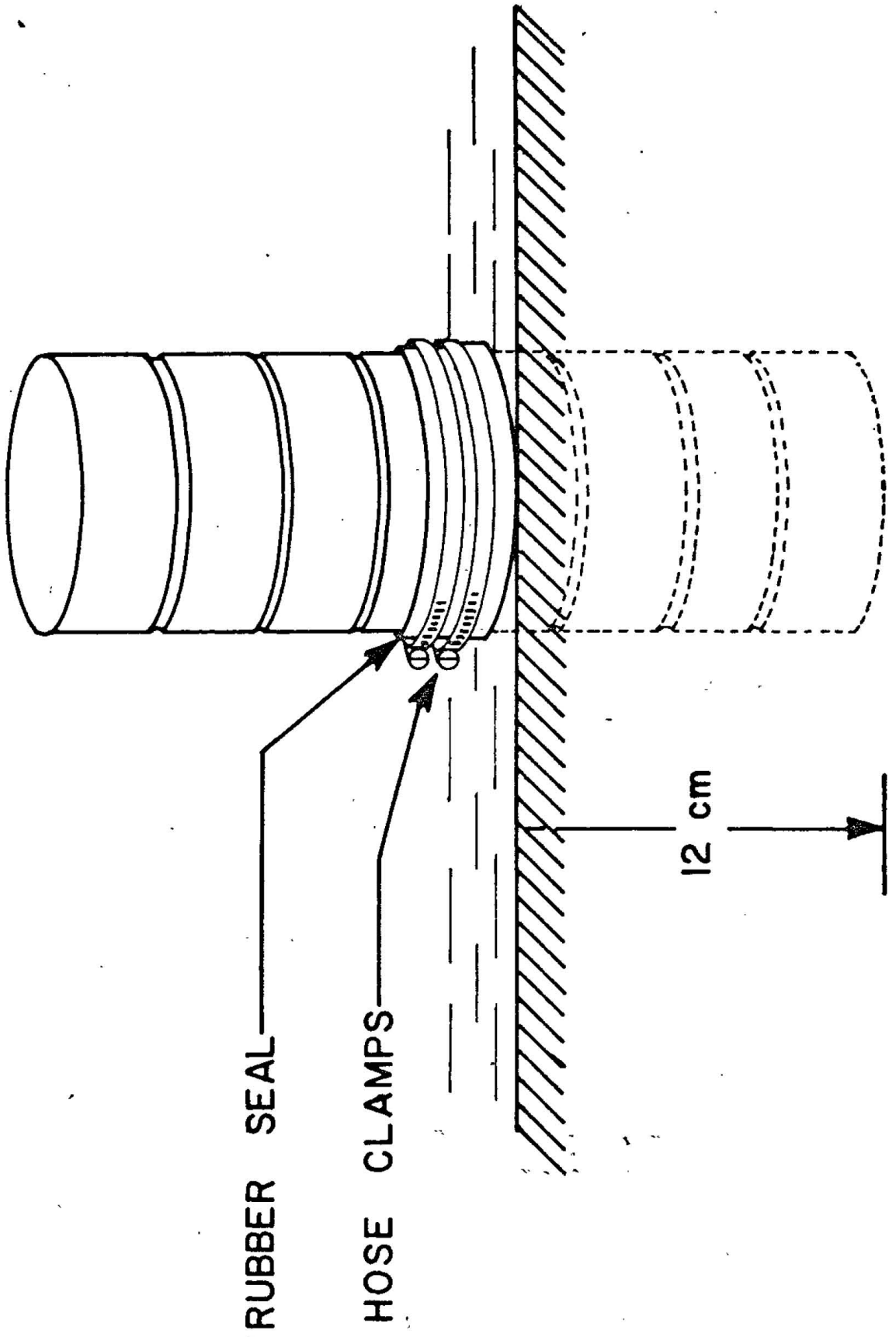


Figure 9


RUBBER SEAL
HOSE CLAMPS
12 cm

plastic lids. SCUBA divers pushed an empty can approximately 12 cm into the sediment to be buried. The cans containing the burial mud were placed over the bottom can by: 1) the top plastic lid was replaced with a tin sheet, 2) the cans and tin sheets were inverted and centered on the can in the sediment, 3) the tin sheet was pulled from between the cans allowing the burial mud to settle onto the sediment, 4) the cans were joined with the rubber and hose clamps previously mentioned, and 5) the remaining plastic lid was removed. Retrieval was accomplished by replacing the plastic lid on the exposed end of the cans, then digging around the bottom can until a plastic lid could be placed on the open end of the bottom can. The entire unit of cans was then carried to the surface.

All experiments were in place for either a 4, 20 or 24 hour duration. Immediately on retrieval the cans were separated by sectioning the contained sediment with the tin sheets. Mud contained in the individual cans was then extruded. The top 5 cm of burial mud in the plexiglas boxes was separated by hand scoops. All samples were sieved through 0.42 and 0.297 mm-mesh screens and preserved with 10% buffered formalin. A dissecting microscope was utilized for sorting and identification of animals.

A Pelecypod-Polychaete assemblage has been well-documented at station K (Sanders, 1960). At the onset of this study a BEBC sample was taken to verify the existence of this assemblage. Since this sample contained the expected assemblage, BEBC samples were not repeated.

Results

In the experiments using plexiglas boxes 5 and 10 cm of mud were dropped on the bottom and sampled after four hours. In every case there was a larger percentage of animals (>.42 mm) left in the bottom than had escaped to the mud layers. The number of species was always greater in bottom mud than in the overlying mud, with one exception. There was not a significant difference statistically however between the number of individuals which had escaped into the burial mud and that remaining in the bottom mud (Tables 5, 6, and 7). The fact that many animals had not climbed out of the bottom mud is not considered significant to their potential survival since they did not appear to have been harmed by burial.

Experiments with cans were initiated because of possible contamination of the burial mud with bottom mud during manipulation of the plexiglas slides. The cans allowed a greater burial depth and were more easily manipulated.

Table 5

Faunal distribution at conclusion of burial experiment

Plexiglas Box
depth of burial: 5 cm
duration: four hours

	>0.42 mm	# of ind.	% of Total No.	<0.42 mm >.297 mm	# of ind.	% of Total No.
			Experiment Ia			
	Nucula annulata	12		Nematoda	50	
	Nephtys incisa	9		Oligochaeta	14	
	Flabelligeridae	8		Aricidea sp.	4	
burial mud	Yoldia sp.	4	30	Ostracoda	4	66
5 cm	Isopoda	2		Nephtys incisa	3	
	Amphipoda	2		Lumbrinereis acuta	2	
	Nassarius sp.	1		Nucula annulata	2	
	Ostracoda	1		Isopoda	1	
				Amphipoda	1	
	Oligochaeta	31				
	Nucula annulata	23		Oligochaeta	27	
	Nephtys incisa	9		Nematoda	12	
	Paraonis fulgens	7		L. acuta	1	44
	Nemertean	5		Nephtys incisa	1	
	L. acuta	3		Paraonis fulgens	1	
	Yoldia sp.	3				
bottom mud	Macoma tenta	2	70			
	Nematoda	2				
	Aphroditidae	1				
	Aricidea quadrilobata	1				
	Ampharetidae	2				
	Nephtyidae	1				
	Paraonis gracilis	1				
	Amphipoda	1				
	Isopoda	1				

Table 5 (Continued)

	>0.42 mm	# of ind.	% of Total No.	<0.42 mm >.297 mm	# of ind.	% of Total No.
			Experiment IB			
	Flabelligeridae	18		Azoic		
	Nucula annulata	17				0
	Yoldia sp.	14				
burial mud	Nephtys incisa	10				
5 cm	Paraonid sp.	3	46			
	Ampherite sp. (?)	2				
	L. acuta	2				
	Isopoda	1				
	Nucula annulata	49		Oligochaeta	22	
	Oligochaeta	7		Nematoda	6	
	Nephtys incisa	5		Nemertean	4	100
	Macoma tenta	5		Nephtys incisa	3	
	Flabelligeridae	4		Paraonidae	2	
bottom mud	Aricidea sp.	4	54			
	Ampherite sp. (?)	2				
	L. acuta	1				
	Ensis sp.	1				
	Amphipoda	1				
	Isopoda	1				

Table 6

Faunal distribution at conclusion of burial experiment

Plexiglas box
depth of burial: 10 cm
duration: four hours

	>0.42 mm	# of ind.	% of Total No.	< 0.42 mm >.297 mm	# of ind.	% of Total No.
			Experiment II			
burial mud upper 5 cm	Yoldia sp.	5		Nematoda	23	
	Nucula annulata	6				
	Nematoda	2	7			22
	Bivalve a	2				
burial mud lower 5 cm	Nucula annulata	11		Nematoda	51	
	Nephtys incisa	11		Nephtys incisa	5	
	Yoldia sp.	5		Oligochaeta	5	61
	Bivalve a	2	14	Paraonid sp.	1	
	Cirratulid sp.	1				
	Macoma tenta	1				
	Paraonid sp.	1				
bottom mud	Nucula annulata	149		Nematoda	12	
	Nephtys incisa	10		Nephtys incisa	3	17
	Yoldia sp.	10		Oligochaeta	2	
	Macoma tenta	4				
	Nassarius sp.	2	79			
	Ensis sp.	1				
	Paraonid sp.	1				
	Lumbrinereid acuta	1				
	Pitar morrhuana	1				

Table 7

Faunal distribution at conclusion of burial experiment

Plexiglas box
depth of burial: 10 cm
duration: twenty hours

	>0.42 mm	# of ind.	% of Total No.	<0.42 mm >.297 mm	# of ind.	% of Total No.
			Experiment III			
burial mud upper 5 cm	Nucula annulata	17		Nematoda	5	
	Yoldia sp.	11		Oligochaeta	5	
	Nephtys incisa	9	23	Nephtys incisa	2	42
	Macoma tenta	1		Flabelligeridae	1	
burial mud lower 5 cm	Nucula annulata	38		Nematoda	10	
	Nephtys incisa	10		Oligochaeta	2	45
	Yoldia sp.	7	34	Nephtys incisa	2	
	Macoma tenta	2				
	Flabelligeridae	1				
bottom mud	Nucula annulata	68		Nephtys incisa	3	13
	Yoldia sp.	2	43	Sipunculida	1	
	Nephtys incisa	1				
	Anemone (closed and full of mud)	1				

Table 8

Faunal distribution at conclusion of burial experiment

Coffee can
depth of burial: 5 cm
duration: four hours

	>0.42 mm	# of ind.	% of Total No.	<0.42 mm >.297 mm	# of ind.	% of Total No.
			Experiment IV			
burial mud	Ostracoda	2	11	Nematoda	2	66
	Nephtys incisa	1				
	Bivalve a	1				
	Cumacean	1				
	Yoldia sp.	1				
	Sipunculida	1				
bottom mud	Nucula annulata	52	89	Oligochaeta	1	33
	Yoldia sp.	3				
	Nephtys incisa	2				
	Lumbrinereid sp.	1				

Table 9

Faunal distribution at conclusion of burial experiment

Coffee can
depth of burial: 10 cm
duration: four hours

	>0.42 mm	# of ind.	% of Total No.	<0.42 mm >.297 mm	# of ind.	% of Total No.
			Experiment Va			
burial mud	Nucula annulata	2		Nematoda	2	18
upper 5 cm	Yoldia sp.	1	8			
	Nephtys incisa	1				
	Nucula annulata	4		Nephtys incisa	1	
	Phyllodocidae a	4		Nemertean	1	18
	Nephtys incisa	2				
burial mud	Yoldia sp.	2				
lower 5 cm	Phyllodocidae b	1	34			
	Bivalve a	1				
	Ostracoda	1				
	Sipunculida	1				
	Nucula annulata	21		Aricidea sp.	3	
	Nephtys incisa	3		Paraonid sp.	2	
bottom mud	Sipunculida	1	58	Oligochaeta	1	64
	Yoldia sp.	1		Nematoda	1	
	Macoma tenta	1				
			Experiment Vb			
	Nephtys incisa	3		Arabellidae	1	
burial mud	Yoldia sp.	1		Nematoda	1	12
upper 5 cm	Apistobranchidae	1	9			
	Ostracoda	1				

Table 9 (Continued)

Experiment Vb (Continued)

	>0.42 mm	# of ind.	% of Total No.	<0.42 mm >.297 mm	# of ind.	% of Total No.
	Nucula annulata	45		Nematoda	6	
	Ostracoda	3		Nemertean	1	44
burial mud	Yoldia sp.	2				
lower 5 cm	Nephtys incisa	1	79			
	Gastropoda	1				
	Lumbrinereid sp.	1				
	Apistobranchidae	1				
bottom mud	Nucula annulata	7	12	Oligochaeta	4	
	Nephtys incisa	1		Aricidea sp.	2	44
				Sipunculida	1	

Table 10

Faunal distribution at conclusion of burial experiment

Coffee can
depth of burial: 10 cm
duration: twenty hours

	>0.42 mm	# of ind.	% of Total No.	<0.42 mm >.297 mm	# of ind.	% of Total No.
			Experiment VIa			
	Nucula annulata	10		Spinonidae	3	
burial mud	Yoldia sp.	2		Minuspio sp.	1	
upper 5 cm	Nassarius sp.	1	28	Oligochaeta	1	11
	Retusa sp.	1				
	Gastropoda a	1				
	Gastropoda a	4		Minuspio sp.	7	
	Nucula annulata	3		Nematoda	4	27
burial mud	Yoldia sp.	3	30	Sipunculida	1	
lower 5 cm	Nephtys incisa	2				
	Minuspio sp.	2				
	Cirratulid sp.	1				
	Nassarius sp.	1				
	Nucula annulata	14		Oligochaeta	10	
	Nephtys incisa	4		Nematoda	7	
bottom mud	Lumbrinereidae	1	42	Paraonid sp.	5	
	Corbula contracta (?)	1		Sipunculida	3	62
	Chlamys sp.	1		Amphipoda	1	
	Ostracoda	1		Ostracoda	1	
				Harpacticoid copepod	1	

Table 10 (Continued)

	>0.42 mm	# of ind.	% of Total No.	<0.42 mm >.297 mm	# of ind.	% of Total No.
			Experiment VIb			
	Gastropoda a	7		Oligochaeta	2	
	Nucula annulata	6		Nematoda	1	7
burial mud	Macoma tenta	4		Minuspio sp.	1	
upper 5 cm	Yoldia sp.	2	23			
	Nephtys incisa	1				
	Pitar morrhuana	1				
	Minuspio sp.	1				
	Nucula annulata	20		Lumbrinereid sp.	2	
	Nephtys incisa	6		Oligochaeta	2	
burial mud	Gastropoda a	6		Cumacean	2	
lower 5 cm	Yoldia sp.	2	39	Minuspio sp.	1	13
	Nassarius sp.	2		Amphipoda	1	
	Minuspio sp.	1				
	Nucula annulata	22		Oligochaeta	32	
	Amphipoda	3		Paraonid sp.	6	
	Minuspio sp.	2		Nematoda	3	
	Cirratulis sp.	2		Nephtys incisa	2	
bottom mud	Macoma tenta	1	37	Mediomastus sp.	2	80
	Ostracoda	1		Harpacticoid copepod	2	
	Glycera sp.	1		Lumbrinereid	1	
	Sipunculida	1				
	Gastropoda a	1				
	Oligochaeta	1				

Table 11

Faunal Distribution at Conclusion of Burial Experiment

Coffee can

Depth of burial: 30 cm

Duration: 24 hours

	> 0.42 mm	# of ind.	< 0.42 > 0.297 mm	# of ind.
		Experiment VIIa		
burial mud upper 15 cm	azoic		Nematoda	1
burial mud lower 15 cm	azoic		azoic	
bottom mud	Nucula annulata	28	Oligochaeta	2
	Macoma tenta	3	Nematoda	1
	Amphipoda	2		
	Flabelligeridae	1	-	
	Nassarius sp.	1		
	Nephtys incisa	1		
		Experiment VIIb		
burial mud upper 15 cm	azoic		azoic	
burial mud lower 15 cm	azoic		azoic	
bottom mud	Nucula annulata	27	Paraonis sp.	1
	Gastropoda	1	Lumbrinereid sp.	1

Again, burial depth of five centimeters did not prevent the fauna from escaping up to the new surface, although only a fraction (11% > .42 mm) did so (Table 8). After four hours of burial under 10 cm of mud, 79% and 34% of the individuals of the 0.42 mm assemblage had moved upward 5 cm while most of the smaller (> 0.297 mm) animals had not apparently moved upward (Table 9). The experiment was repeated with a twenty hour duration.

At the conclusion the > 0.42 mm population had become evenly distributed throughout the sediment column (Table 10). Burial under 30 cm of mud prevented any upward movement of animals during the twenty-four hour duration of the experiments (Table 11). Rapid decomposition of small soft bodied organisms may account for the small number of organisms found in the bottom mud.

Discussion

Although the sediments are homogeneous (Driscoll, Clifford, Rowe and Young, in prep.) there is a natural patchiness in the benthic fauna which cannot be controlled. To estimate how this would be reflected in the burial experiments, umpublished data from seven BEBC samples collected at Station K in November, 1972, can be cited. The mean number of species contained in each 445 cm^2 sample

was 25 ± 2.9, S.E.M. = 1.2. The dominant species by numerical abundance was Mediomastus ambiseta, a polychaete. The mean number of individuals per sample was 1481 ± 112, S.E.M. = 445. The second most abundant species was Nucula annulata, a bivalve. The mean number of individuals present was 178 ± 28, S.E.M. = 11. The total number of organisms in each sample averaged 2012 ± 1346, S.E.M. = 549. Thus, although the number and type of species present is homogenous, the numerical abundance of all individuals in the assemblage fluctuates considerably.

The variance to mean ratio can be used to approximate patchiness. With a random dispersion of individuals on the bottom, $v/\bar{x}$ should be about 1, if the fauna is evenly dispersed it will be less than one, but when it is patchy or clumped, it is greater than one (Pielou, 1967). The Buzzards Bay fauna, according to these data, is highly patchy ($v/\bar{x} = 900$). These data on patchiness were collected in November, 1972, and contain predominantly Mediomastus ambiseta, a highly seasonal member of the fauna. The burial experiments were done in June and July, 1974, and no Mediomastus was present. Exclusion of Mediomastus from the earlier series still resulted in a patchy fauna distribution

($\bar{x}$ = 531, $v/\bar{x}$ = 13). This uncontrolled variability in faunal data must be considered to have an effect on the results of the burial experiments.

Faunal patchiness causes the number of species and animals manipulated in any one experiment to vary. While the mean number of species found was 12 $\pm$ 5, S.E.M. = 1.4, the mean number of individuals found in the experimental systems was 140 $\pm$ 110, S.E.M. = 3. This variability is consistent with the observed patchiness at St. K and prevents any meaningful statistical or mathematical (diversity) calculations. For example, species diversity based on all animals present for experiments IV and VII indicate that experiment VII had a greater diversity (1.17 and 1.22) than experiment IV (0.9), yet no large (>.42 mm) and only one small (>0.297 mm) animal escaped burial in experiment VII.

What specifically precipitates an escape response is not known and variations in an individual animal's condition may influence how long the organism will endure burial before attempting to escape, as well as the probability of a successful escape. Such variations may explain the absence of definate patterns in the experiments. Both experiment II and V were 10 cm burials for four hours. At the conclusion 149 Nucula annulata (90%) remained in the bottom mud of experiment II and 17 individuals (10%) had attempted escape. In experiment Va 22% of the Nucula, 6 individuals, had

escape, while 86% (48 individuals) had attempted escape in experiment Vb.

Thus, analysis of the results of in situ burial becomes somewhat subjective. After consideration of the physical appearance of the animals, as well as their numerical distribution, it seems that in situ burial with native sediment of 10 cm or less does not significantly affect the polychaete-pelecypod infauna community. Animals in such assemblages apparently possess the ability to obtain a viable position in the sediment column.

A possible explanation for the inability of the fauna to escape 30 cm of burial mud is that the animals could not tolerate anoxic conditions in the burial mud. If this explanation were valid, however, dead animals should have been found in the burial mud. Since no animals had even attempted to escape it appears that at some critical depth of burial, some phenomenon such as compaction or pressure inhibits any movement at all.

Bryant, Deflache and Trabant (1974) have shown that "void ratio - log effective pressure curves" for marine clays are linear. The void ratio (the ratio of interstitial space to volume of solid matter) of abyssal clays (initial void ratio range: 2-3.75) from the Gulf of Mexico

decreased about 0.5 when pressure was increased from .02 to .07 kg/cm^2. Assuming a sediment density of 2 g/cc, 30 cm of burial mud would increase pressure on the bottom sediment by .06 kg/cm^2 with a corresponding decrease in void ratio. Such a decrease in void ratio means that the organisms have smaller interstitial spaces through which to move, thereby increasing the effort necessary to escape. It appears that the escape ability of benthic organisms may be regulated by the amount of compaction of the burial mud. This explains the lack of upward movement found by Kranz and this work when burial depth exceeded the upper escape limit.

NATURAL SEDIMENTATION

For the past six years the Sahelian zone of West Africa has experienced a severe drought. The boundaries of the Sahara Desert are extending at a reported rate of 30 miles/yr (Wade, 1974) and prevailing northerly winds carry large quantities of sand out to sea. From 5 to 13 x $10^6 m^3$ of sand were estimated to move across an 80 km line from Cap Blanc east into Spanish Sahara, meaning that the region of ocean called Banc d'Arguin in Mauritanian receives this material, some of which is presumed to escape to the deep-sea via the submarine canyons bordering this semi-enclosed bay system (Sarnthein and Walger, 1974; Senin, 1974). Ships traversing the region are quickly covered with a layer of sand, and water turbidity is quite high due to the terrigenous material in the water column. During the first half of 1974 the JOINT I project of CUEA studied the upwelling phenonmenon which occurs off the Spanish Sahara coast. Samples collected by the Mauritanian trawler R/V ALMORAVIDE in early May, 1974 and late May by R/V ATLANTIS II were analyzed to ascertain the effect of high water turbidity and high sedimentation rates on the benthic faunal community structure.

Methods

All benthic faunal samples were collected during R/V Atlantis II Cruise 82, leg 4. A 0.1 m^2 van Veen grab was used to obtain samples from four stations (figure 10). The grab samples were sieved through a 0.42 mm-mesh screen. Those animals retained on the screen were fixed with 10% formalin buffered with sodium borate. Preserved samples were elutriated in the lab; the sediment residue was examined with a dissecting microscope to ensure complete removal or organisms. Elutriated material was split with a Folsom sample splitter (McEwen, Johnson and Folsom, 1954). Usually the sample was split 3 times, resulting in one-half and two quarter samples. The quarter samples were sorted individually and then lumped together. A few very large samples were split to one-eights and two eights were sorted. A dissecting microscope was used to sort the animals to species. Wet weight biomass was obtained by blotting the animals on a paper towel for two minutes and then weighing them on a Mettler microbalance. After weighing, the animals were stored in 70% ethanol. Nematodes were dehydrated in glycerin and then fixed in glycerin mounts for identification. Biomass of nematodes was not estimated.

Shannon-Wiener Information Function was used to determine species diversity. Evenness of distribution (E/S) was also determined as previously described. Percent similarity was determined by the index of Whittaker and Fairbanks (1958):

$S = 100 - 0.5 \Sigma \left| P_{ij} - P_{ik} \right|$ where n = total number of species, P_{ij} and P_{ik} are proportions of the i^{th} species in the j^{th} and k^{th} samples.

Figure 10. Approximate bathymetry and station locations off Spanish Sahara.

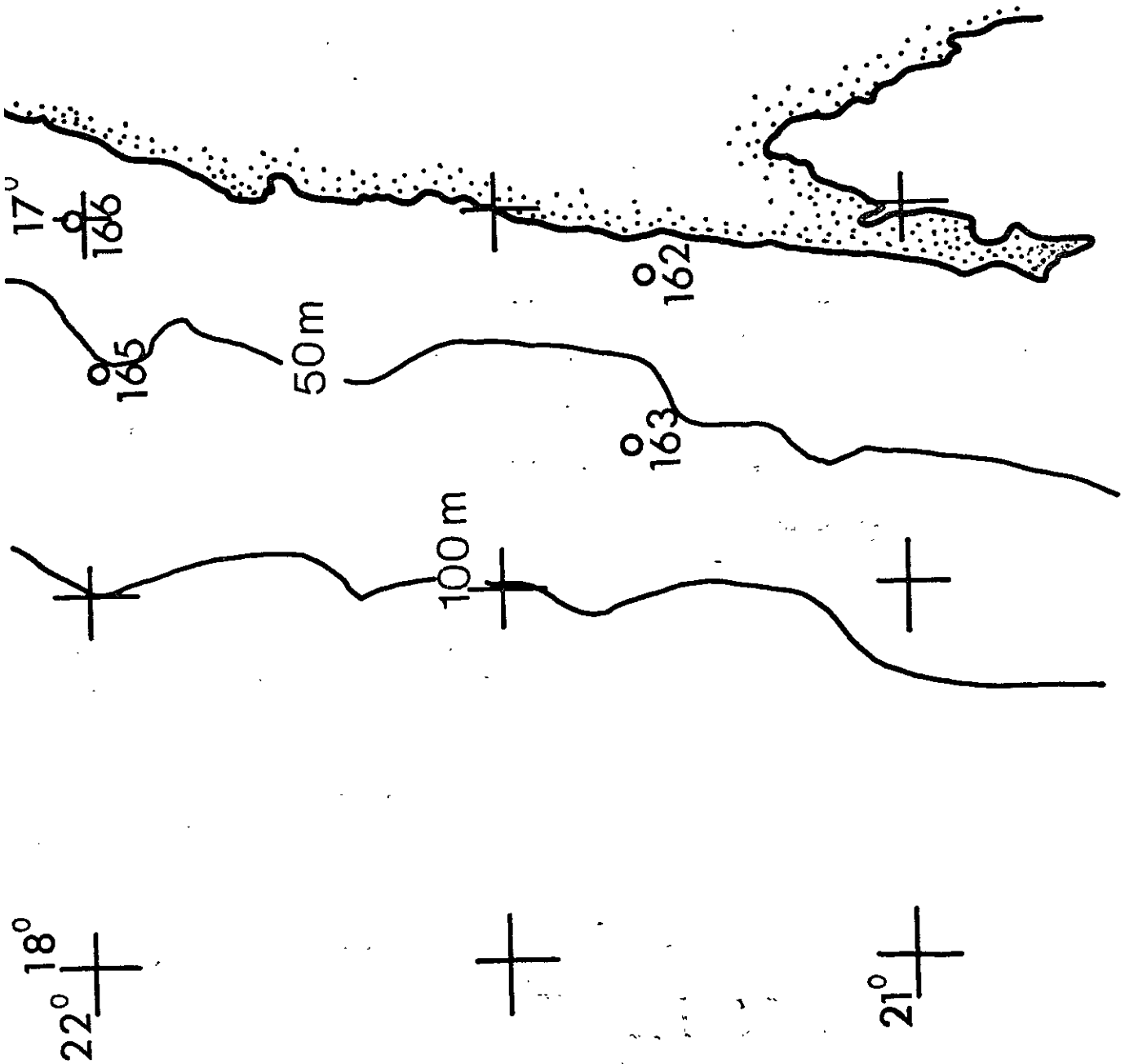


Figure 10

Suspended sediment samples were obtained by filtering surface and near-bottom water samples until sediment was visible on the filter. The volume of water filtered was recorded. Analysis of the samples was performed by J. D. Milliman and is reported elsewhere (Milliman, in prep.). Bottom sediment samples for analysis of grain size, organic content, and pore water nutrient content were obtained with a pantograph box corer. Description of these analyses are reported in Rowe, Clifford, and Smith (in prep.).

Sedimentation rates have been estimated from data collected by Rowe, Clifford and Smith (in prep.), using arrays of sediment traps suspended at various heights off bottom.

Results

A complete faunal list is contained in Appendix III. Numerical abundance at nearshore stations was an order of magnitude less than at the midshelf stations. Total biomass

showed greater variability than numbers. Mean biomass was greater at the midshelf stations. However, the range of biomass at nearshore stations was not significantly different from the midshelf range (Table 12). The number of species present in a sample tended to be greater at the midshelf stations but was not statistically separable by students and test from nearshore stations (average of 49 vs. 40).

Midshelf samples were dominated by the polychaete species Spio sp. a. In all except one sample this species composed 34 - 54% of the population while the next most abundant species contributed 8 - 16%. The one exception is sample 165-1 where Spio sp. a. was the most abundant species but contributed only 12% of the total number of individuals. In the nearshore samples no one species contributed more than 18% of the total numerical abundance. Spio sp. a was always one of the three most abundant species in the samples. Other abundant species were Spio sp. b, Onuphidae sp. a, and Tanais sp. a.

Nearshore biomass was dominated by the bivalve Tellina sp. At the northern station the polychaete Onuphidae sp. c and the decapod Pagurus pollicarus also made major contributions to the total biomass. Northern midshelf station biomass was dominated by a holothurian of the Order Dendrochirota, while southern samples were variously dominated by the polychaetes Tharyx sp., Cirratulid sp. c, Cirratulis sp.

Table 12

Number of Species, Individuals, and

Total Biomass for Each Sample

(1/10 m^2 van Veen, > .42 mm)

Station	Depth (m)	Total no. per sample	Total biomass (mg)/sample	No. of species
		Nearshore		
162	39	336	1753.5	28
		883	2896.2	45
		576	2803.7	39
166	35	704	3313.7	55
		678	764.6	35
		Midshelf		
163	62	2181	1628.8	45
		2048	1804.9	35
		3248	782.5	50
165	57	2220	11584.0	55
		2402	3372.2	60

and a sipunculid.

Diversity based on numbers was greater nearshore (Table 13). One exception, midshelf sample 165-1, had a greater diversity because of a decrease in numerical abundance of a single polychaete species, Spio sp. a. Since numerical abundance and number of species was greater at the midshelf stations, greater nearshore diversity must result from even distribution of individuals between the species present. Nearshore station E/S values based on numbers were always greater than 0.53 while midshelf values were, with one exception, less than 0.25 (Table 13). Biomass diversity ranged between 1.5 and 2.6 and E/S values between 0.08 and 0.278 at all stations and showed no clear trends.

Results of the percent similarity index based on numbers indicated that all midshelf samples were 29-55% similar, nearshore samples ranged between 32% and 41% similar. Northern midshelf samples were between 30-40% similar to northern nearshore samples. Southern midshelf samples were 21-33% similar to southern nearshore samples. Nearshore southern samples ranged between 41% and 56%, while midshelf samples were between 56% and 71% similar. The northern nearshore samples were 47% similar, while the midshelf samples were 65% (Figure 11).

Table 13

Diversity and Evenness Values calculated for each sample off Spanish Sahara*

		Nearshore			Mid-Shelf	
		#	biomass		#	biomass
H	166	3.020	2.266	165	3.671	2.267
E/S		0.569	0.268		0.678	0.166
H		3.403	1.513		2.423	2.126
E/S		0.537	.081		0.188	0.140
H	162	3.213	2.056	163	2.183	1.511
E/S		.621	.195		.189	.096
H		3.229	2.068		2.047	1.524
E/S		.549	.172		.215	.127
H		3.062	1.680		2.519	2.713
E/S		.737	.185		.234	.284

* Does not include oligochaetesas they were not sorted to species.

Table 14

Suspended Sediment Analysis

	Station #	Water depth	Sample depth	Total suspended matter (mg/l)	% terrigenous	Wt. terrigenous mg/l	Wt. organic mg/l
Nearshore	162	39	0	1.10	60	0.37	0.73
	162	39	35	0.68	50	0.19	0.49
	166	35	0	0.92	>90	0.04	0.90
	166	35	34	1.08	>85	0.09	0.99
Midshelf	163	62	0	0.78	<10	0.02	0.76
	163	62	60	0.22	<10	0.00	0.22
	165	57	0	0.45	<10	0.01	0.44
	165	57	54	0.25	<< 5	0.00	0.25

Figure 11. Schematic representation of percent similarity between samples from NW coast of Africa.

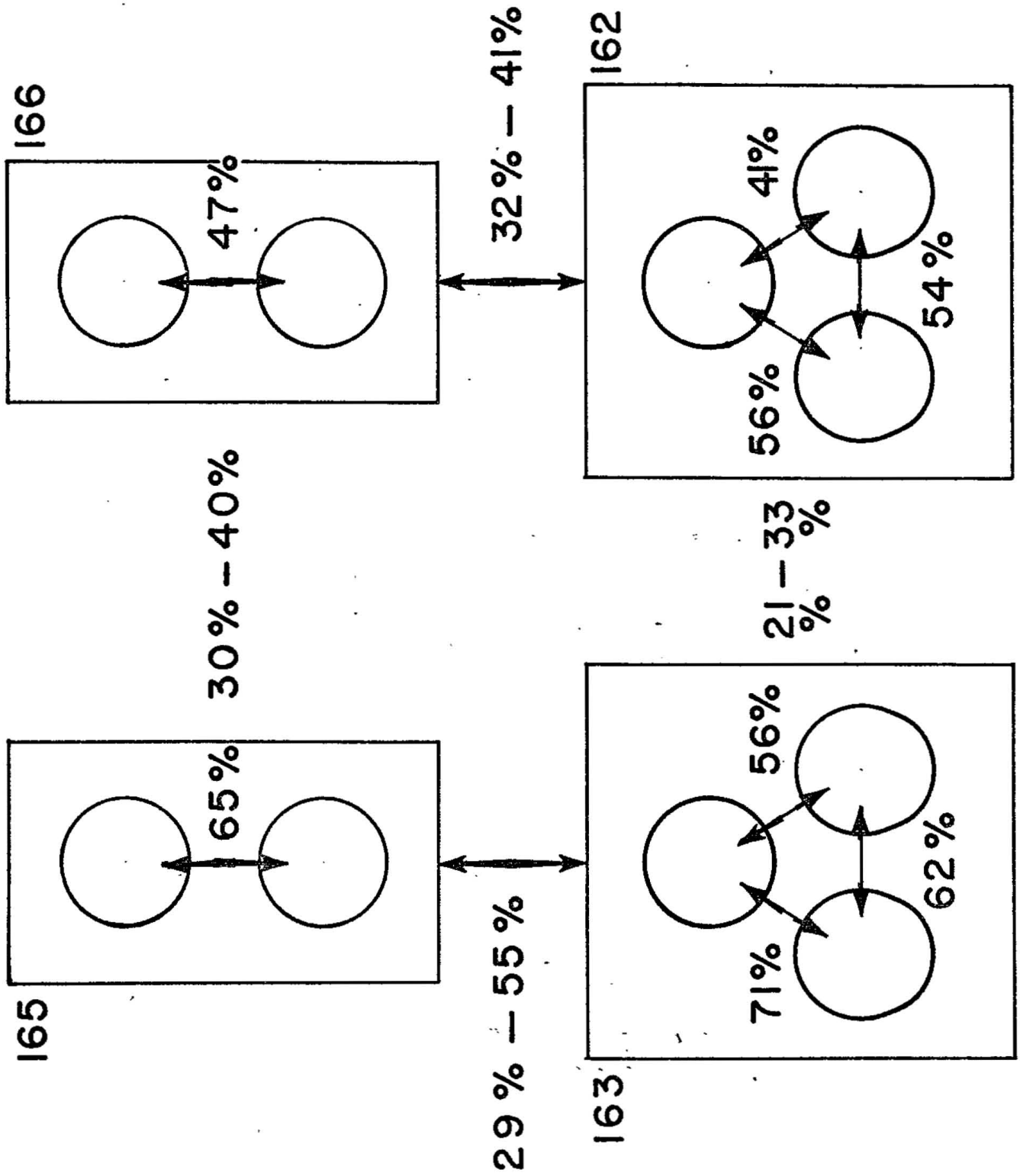


Figure II

Suspended sediment data are listed in Table 14. Samples from the nearshore stations contained 50% or greater terrigenous material, while the midshelf stations had less than 10% terrigenous material in the suspended matter. The total weight of suspended material at the nearshore stations was twice that found at the midshelf stations. Weight of organic material suspended in the bottom water at the nearshore station was more than twice that found at the midshelf stations. Deposited sediment at the nearshore stations had less organic carbon and nitrogen than that of the single midshelf station where they were measured (Table 15). Organic carbon and nitrogen concentration, and fish, zooplankton and benthos biomass all were highest along the shelf-slope break, presumably reflecting the higher primary productivity there (Rowe and Driscoll, Submitted; and Haedrich, Blackburn and Bruhlet, Submitted). Grain size and $CaCO_3$ composition was similar for the northern stations while the southern nearshore station had a greater clay content and lower $CaCO_3$ composition (Table 15).

Sediment trap data from nearshore off Cap Blanc are contained in Table 16. The average rate for all traps higher than one meter above the bottom was 25.43 g/hr m^2. Assuming a sand sediment density of 2.5 g/cc gives a

sedimentation rate of 10.2×10^{-4} cm/hr or 8.9 cm/yr. Since the prevailing winds blow strongest during the day and all measurements were made during daylight, the measured rate may be higher than the actual rate. If the actual rate is arbitrarily assumed to be one half the measured rate, the result (4.4 cm/yr) is still a high rate of sedimentation.

For comparison data collected in Buzzards Bay using similar sediment traps is also presented in Table 16. Clay sediment density was assumed to be 2 g/cc resulting in an average sedimentation rate of 4.55 mm/yr or an order of magnitude less than the rate off Cap Blanc. The latter value is higher than the average rate based on the age of Buzzards Bay and the total depth of its sediment (1.5 mm/yr, Hough, 1940), but agrees well with the thickness of layering in its upper few centimeters, prior to much compaction.

Table 15

Deposited Sediment Analysis

		% sand	% silt	% clay	% $CaCO_3$	% C	% N	C/N
Nearshore	162	85	8	7	59	.92	.10	9.2
	166	90	7	3	72	0.61	0.09	68
Midshelf	163	sediment sample not taken						
	165	96	4	0	84	2.16	0.03	72

Table 16

Sediment Trap Data

Date	Meters off Bottom	Time (hrs)	Rate (g/hr m^2)
JOINT I			
April 74	1	12	$\bar{x}_2 = 216.43$
April 74	2	12	$\bar{x}_2 = 22.11$
May 74	2	4	$\bar{x}_2 = 15.19$
May 74	3	4	$\bar{x}_2 = 13.07$
May 74	4	4	$\bar{x}_2 = 8.00$
May 74	2	4.5	$\bar{x}_2 = 62.20$
May 74	3	4.5	$\bar{x}_2 = 32.01$
BUZZARDS BAY			
July 73	2	4.5	$\bar{x}_2 = 3.92$
July 73	3	4.5	$\bar{x}_2 = 2.86$
August 73	2	3.5	$\bar{x}_2 = 1.82$
August 73	3	3.5	$\bar{x}_2 = 0.70$
January 74	1	6	$\bar{x}_2 = 1.85$
January 74	2	6	$\bar{x}_2 = 0.75$
January 74	3	6	$\bar{x}_2 = 0.90$
July 74	3	5	$\bar{x}_4 = 0.41$
September 74	3	4	$\bar{x}_4 = 0.36$
November 74	3	4	$\bar{x}_4 = 0.01$

Discussion

Benthos off Cap Blanc, Spanish Sahara, are exposed to two types of unpredictable fluctuations in small time- and space-scales: sedimentation (which is composed of both high sedimentation rates and high bottom water turbidity), and upwelling. Upwelling, because of variations in productivity or food supply, may act synergistically with sedimentation stress. The physical phenomenon of offshore winds carrying terrigenous material to sea occurs constantly while upwelling processes vary over time and space (Codispoti, in prep.). The most intense upwelling is located at the shelf-break region. High sedimentation rates dominate the nearshore environment (Rowe and Clifford, in prep.). Sedimentation rates reported for the nearshore environment (approx. 8 cm/yr) are less than those that prohibited escape from burial as discussed in the previous section. The constant expenditure of energy to escape burial could explain the observed small size of individuals, but species should not have been eliminated from the community by burial, but rather from competitive exclusion, with the competitive advantages being accrued by species best able to cope with burial, sediment instability and high turbidity.

If stable (biologically accomodated) communities are characterized by larger diversity values and more even distribution (E/S), then the nearshore communities off Cap Blanc are more biologically accommodated than the midshelf stations (based on numbers). This result was not expected since the nearshore stations were thought to be subject to greater stress.

Lower diversity values at midshelf stations were caused by the dominance of one polychaete species, a spionid, Spio sp. a. Two other spionid species were also found in great numbers at these stations. Spionid polychaetes are known to feed by extending their palps into the water column and randomly waving them. Organic material collected by the palps is scraped off and ingested by the animal (Long, pers. comm.). This type of feeding would not be advantageous where a high concentration of terrigenous material is suspended in the bottom water and could account for the lower abundance in spionids nearshore.

Further evidence that feeding type influences community structure is seen in the nematode fauna. Nearshore the number of large nematodes (retained on a 0.42 mm-mesh screen) was very low. Samples 162-1 contained no such nematodes and the remaining four samples never had more than 12. Midshelf samples contained from 42 to 272.

Wieser (1952) has described four groups of nematodes based upon buccal structure. Types 1a and 1b are composed of organisms with small unarmed buccal cavities; types 2a and 2b are organisms with armed buccal cavities and some species are capable of extending the teeth out of the mouth. Types 1a and 1b dominate in soft mud and organic-rich sand sediments, while types 2a and b dominate in organically-poor sand (Wieser, 1952).

All nematodes found in the nearshore samples were members of Wieser's type 1 group while the majority of the species represented in midshelf samples were type 2 organisms. Type 1 nematodes probably feed by sucking organic material off the larger mineral particles and aggregates in the sediment. Their small buccal cavities prohibit the ingestion of large mineral particles which could cause mechanical damage, while admitting fine organic material contained in interstitial spaces. Type 2 nematodes are carnivores, actively seeking prey in the interstitial spaces. Their directed search apparently results in more efficient food-gathering in the organic-poor and larger interstitial space environment of the midshelf region.

It was assumed that environmental stress should be greater at the nearshore stations due to the constant high sedimentation rate. However, diversity indices would indicate that the midshelf region is subject to the greater stress. This suggests that variability of stress is more important than absolute magnitude.

Although the samples were collected during a short time interval (three days) and represent one point in time it can be inferred that on an ecological time scale the midshelf region is subject to greater unpredictable variations of the environment than the nearshore region. With increased distance from shore the probability of a constant large-quantity of terrigenous material being deposited is decreased while the possibility of being affected by the intense shelf-break upwelling increases. Although the high primary productivity should supply the bottom with large amounts of organic matter, terrigenous sedimentation so dominates that an organically-poor sediment results. As the intensity of upwelling fluctuates the supply of organic material to the midshelf benthos should vary. It may be these unpredictable conditions which caused the community to become dominated by a polychaete species, presumably able to adjust to the environmental unpredictability.

Although most experimental work tested the hypothesis that competitive exclusion is prevented by predators, it appears that the physical environment, by preventing the proliferation of Spio A, prevented "competitive exclusion" or an uneven distribution among the species.

As the species list lengths were not different, the offshore decrease in diversity was not the result of competitive exclusion, but rather due to the proliferation of an opportunist utilizing an available, although unpredictable, resource.

Under constant environmental stress the species composition of the nearshore communities has become one of organisms whose physiological tolerance limits are apparently not exceeded by the environment. The community that has evolved does not respond to the natural sedimentation as a stressful condition.

Chapter IV

SUMMARY AND CONCLUSIONS

An assemblage of organisms can be characterized by the term "community". Several definitions of the term have been proposed. The concept of community used in this work is that of Mills (1969): "a group of organisms occurring in a particular environment and interacting with each other and with the environment and separable by means of an ecological survey from other groups". The three components of community structure considered are abundance of individuals and species, biomass of individuals, and species diversity.

Species diversity can be considered to be of two types. Equilibrium diversity results when a community has been exposed to stable conditions over epochs of geologic time. Sander's Time-Stability Hypothesis (1968) explains the evolution of equilibrium diversity. In addition a transient diversity structure exists which is the product of biological interactions and fluctuations in the environment which occur on an ecological time scale. Such fluctuations can be caused by pollution or natural changes in the environment. The diversity portion of this study is focused on the influence of natural short-term fluctuations in environmental parameters on transient diversity.

The effect of low dissolved - oxygen on transient benthic community structure was studied with samples from Golfo Dulce, an intermittently anoxic basin off the west coast of Costa Rica and the Fosa de Cariaco, an anoxic trench off the north coast of Venezuela, and compared to work in the San Diego Trough (Jumars, 1974). The periodic flushing of Golfo Dulce exposed the benthic community to short-term fluctuating oxygen concentrations. The result was a community numerically dominated by the polychaete species Paraonis lyra, a very small organisms. Species diversity was also low. This contrasts with samples from outside the basin where the available oxygen was low but presumed more constant than that inside the basin. Here the organisms were an order of magnitude greater in size. The individuals present were more evenly distributed among the species represented resulting in a larger diversity value outside the basin.

The Fosa de Cariaco is an anoxic basin which is subject to seasonal fluctuations in the depth of the anoxic water. Samples taken in the interface region (between oxic and anoxic waters) contained a few more species and individuals than samples from Golfo Dulce. Diversity values were greater than those from Golfo Dulce because of the more even distribution of individuals among the species represented.

Conditions in the San Diego Trough appear to be highly stable, on an ecological time scale, with low dissolved-oxygen concentrations year-round. Samples from the trough contained highly diverse assemblages with numerical abundances and biomass similar to that expected from a region of similar physical characteristics and much higher oxygen concentrations.

In contrast to fluctuating oxygen conditions which eliminated many species from the community, in the presence of fluctuating amounts of suspended matter in the bottom water the total species length was maintained. High rates of terrigenous sedimentation occurring naturally off the Spanish Sahara coast produced extremely turbid bottom water conditions which apparently hampered the feeding of spionid polychaetes. Further offshore where the quantity of terrigenous material reaching the bottom was less and presumably less predictable, the spionids were able to flourish. The result was greater numerical abundance and biomass offshore and a lower transient diversity value, all of which was directly attributable to increases in the spionid population.

Results of simulation of catastrophic burial by in situ burial of small isolated portions of Buzzards Bay sediment indicated that burial of 10 cm or less does not

significantly affect polychaete - pelecypod infauna assemblages. Individuals of all species were capable of escaping up through the sediment. The constant high sedimentation rate off Spanish Sahara provided a natural burial situation, with daily burial depths less than those shown to prohibit escape. The small size of the organisms living under these conditions may have been a result of the constant expenditure of energy for escape.

The structure of benthic communities has been characterized by three parameters: numerical abundance, biomass, and species diversity statistics. Numerical abundance tended to be greater in regions of fluctuating conditions although the size of the individual organisms was small. Biomass did not have a definative pattern of distribution. Total community biomass can be assumed to be a function of the resources available, and one could conclude, as others have (Hessler and Jumars, 1974) that there is little relationship between diversity, and abundance and biomass.

In regions of fluctuating environmental conditions diversity values are low, principally because of dominance by a few or single species. Increasingly predictable conditions, even though stressful, can result in a more even distribution of individuals among the species present and a

correspondingly high transient diversity value. This may result because one species is prevented from proliferating, such as occurred nearshore off Spanish Sahara, or because more species are able to adapt to the stable "stressed" environment.

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PREFACE TO APPENDICES

Animals were identified with the aid of published keys and species descriptions. As the intent of this study was to determine the different types of species occurring in an area, letter designations were used to denote different species when the author could not be confident of specific identifications from the information available. Even when species names were given, no zoogeographic interpretations were intended and none should be assumed. The samples are preserved in alcohol and are available to those wishing to pursue zoogeographic studies.

Appendix I

Species List from Golfo Dulce

Species data are presented in the following format:

Station No.	1	1
Grab	A	B
Species* name		X Y
Species name		

X = number of individuals present in 0.1 m^2 sample

Y = biomass (wet weight, mg) of individuals present in van Veen grab sample

Blocks with biomass values and no numbers are fragments of the family found in the sample.

* Indicates organisms not included in diversity calculations.

Station No.	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Colenterata																										
Anemone															2											
sp															4.6											
Nematoda													12		2	1	4									
sp													-		-	-	-									
Nemertea																										
Nemertean														2	2											
sp															19.8											
Oligochaeta*													4													
sp													-													
Sipunculida														2												
sp														0.2												
Pareulepidae																										
Pareulepis																	1									
sp																	12.2									
Phyllodocidae																										
Eteone													4													
sp													0.4													
Pilangidae																										
Sigambra														4											3	
tentaculata														1.0											0.9	
Syllidae																										
Exogone													4													
sp													0.4													
Nereidae																										
Ceratonereis																1										
sp																11.7										

Station	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Nereidae																										
Nereis sp													12 17.6	1.2	2 1.0		1 7.6									
Nephtyidae																										
Nephtys sp																									2 304	2 9.3
Goniadidae																										
Glyeinde armigera															6 7.6	8 13.2	3 4.0	1 1.4								
Onuphidae																										
Onuphis sp													8 1.2	29.0		2 5.5										
Eunicidae																										
Eunice Schema-cephala													5.0	6 13.0												
Lumbrineridae																										
Angeneria sp													4 76.4													
Lumbrineris acuta																4 1.5										
Lumbrineris inflata													64 14.0		8 3.2	1 0.4										
L. latreilli																5 14.9										
L. moorei															8 0.6											

Station No.	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab Letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
L. zonata														44 10.6												
Ninoe fusca															2 0.2											
Ninoe gemma																1 0.4										
Ninoe sp a													4 0.4													
Ninoe sp b													4 0.4													
Lumbrineridae fragments												92.4	1.2	0.2		3.3										
Arabellidae Arabellida sp													2.4	0.2											2 8.7	
Arabellidae c.f. Notocirrus californiensis																	2 0.1									
Dorvilleidae genus species													4 0.4													
Questidae genus species													4													
Paraonidae Paraonides lyra													544 64.4	190 24.6	4 0.2										20 2.5	

Station No.	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Paraonidae Paraonides sp a													4													
Paraonidae Paraonides sp b													20 0.5													
Cirratulidae Acrocirrus sp															2 1.2											
Cirratulidae Chaetozone sp															2 0.2											
Cirratulidae c.f. Tharyx epitoca															4 2.8											
Cossuridae genus sp													12 2.4		4 0.6											
Flabelligeriidae Pherusa sp														6 62.6	2 1.0		5.4									
Capitellidae Meidomastus sp															4 16.2											
Maldanidae fragments													6.4			10.5										
Ampharetidae fragments															35.0											

Station No.	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Terebellidae																										
Polycerine													4													
sp													0.4													
Sabellariidae																										
Sabellida													4	2												
sp													0.8	119												
Cirratulidae																										
Cirratulus														2	24											
cirratus													57.2	42.6		4.6		0.3							1.6	
Cirratulidae																										
C.													48		4	4										
sp a													4.0		3.4	2.1										
Cirratulidae																										
C.													16													
sp b													0.8													
Cirratulidae																										
Cirriforma													4													
spirabrancha													0.4													
Cirratulidae																										
Tharyx															4											
marconi															198.2											
Cirratulidae																										
Tharyx																2										
monilaris																1.2										
Cirratulidae																										
Tharyx													116	56		1										
multifilis													10.8	8.6		26.8										
Spionidae																										
Pygospio															4											

Station No.	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Spionidae Spionid sp														2 1.2 3.2												
Spionidae genus sp													4 1.2												2 0.5	4 0.7
Spionidae Nerinides Maculata																										
Serpulidae e.f. Vermil- iopsis multi annulata														2 0.2												
Echinodermata Ophiuroid fragment															155.8											
Pelecypoda Adrana sp																									1 3.5	
Pelecypoda Caspidaria costata															2 6.8											
Pelecypoda Glycymeris sp															2 1.8											
Pelecypoda Nucula scheneki																										1 51.0
Stomatopoda Reteaus													8	4												

Station No.	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Cumacea Lenconidae endorella																	1 0.1									
Isopoda Paranthura elegans															2 15.6	2 2.1										
Amphipoda Corophium Bonelli Milne																		1 0.7								1 4.4
Amphipoda Ericthonius sp					2 5.9	1 1.3			2 11.3					1 18.6			1 1.8									1 0.5
Amphipoda Lyssianassid genus species															4 1.2											
Amphipoda Calliopiidae gr sp																				1 0.1						
Amphipoda Cerapus sp																								1 0.3		
Amphipoda Deutella californica															2 1.2											
Amphipoda Periotripus brevis															28 3.6	20 2.6										

Station No.	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Amphipoda Ampithoe sp																1 0.1										
Amphipoda Mandibulo- phous sp																6 6.3										
Amphipoda Talitroidea genus species																3 5.1										
Decapoda Callianassa major															4 28.4											
Decapoda Carcinoplaci- nae genus sp														22 117	76	2 10.0										
Vertebrata* Conger congrus															1 41	23.5										
Vertebrata Phoronis sp																1 0.5										

Appendix II

Species list from Fosa de Cariaco

The following information is given for each species at station 2027 and 2028:

1) number of individuals present in 0.2 m^2 van Veen grab sample,
2) % numerical composition of total sample,
3) biomass (wet weight, mg) of individuals present in 0.2 m^2 van Veen grab sample,
4) % biomass composition of total sample.

Species data for station 4 are presented in the following format:

Species name	Sample
Species X	x
	y

x = number of individuals in 0.1 m^2 van Veen grab sample

y = biomass (mg) in 0.1 m^2 van Veen grab sample

Biomass only is given for fragments.

Numbers only are given for nematodes.

* Indicates organisms not included in diversity calculations.

AII 79 Station 2027

Group	Number of individuals	% comp	biomass (mg)	% biomass
Nematodes				
Filoncholaimus n.sp.	1	.29	-	-
Cyatholaimidae	1	.29	-	-
Desmocolecidae	1	.29	-	-
Nematoda genus a	1	.29	-	-
Polychaeta				
Polyodontidae	1	.29	0.2	.05
Leanira sp.	3	.88	9.1	2.12
Exogone dispar	1	0.29	-	0.00
Exogone sp.	8	2.35	-	0.00
Exogonella longipedata	1	0.29	-	0.00
Streptosyllis sp.	1	0.29	1.2	0.28
Aglaophamus sp.	2	0.59	46.9	17.88
Micronephtys minuta	1	0.29	0.1	0.02
Nephtys bucera	1	0.29	0.5	0.12
Nephtys squamosa	42	12.32	2.4	0.56
Nephtys sp.	1	0.29	2.6	0.60
Ephesiella sp.	1	0.29	1.0	0.23
Glycera capitata	1	0.29	1.5	0.35
Goniada brunnea	2	0.59	7.0	1.63
Goniada sp.	9	2.64	2.8	0.65
Lumbrineris acuta	10	2.93	15.9	3.70
Lumbrineris latreilli	1	0.29	1.6	0.37
Lumbrineridae gn. sp.	1	0.29	0.1	0.02
Arabella sp.	3	0.88	1.1	0.26
Drilonereis longa	1	0.29	-	0.00
Drilonereis sp.	4	1.17	0.3	0.07
Minuspio cirrobranchiata	15	4.40	1.6	0.37
Pygospio sp.	1	0.29	0.4	0.09
Scolelepis sp.	1	0.29	-	0.00
Spiophanes bombyx	1	0.29	0.2	0.05

AII 79 Station 2027 (cont'd)

Group	Number of individuals	% comp	biomass (mg)	% biomass
Spiophanes sp.	1	0.29	0.2	0.05
Orphyrotrocha	3	0.88	0.5	0.12
Aricidea albatrossae	2	0.59	0.4	0.09
Aricidea belgicae	7	2.05	0.1	0.02
Aricidea jeffreysii	1	0.29	0.2	0.05
Aricidea neosuecica	8	2.35	-	-
Aricidea quadrilobata	9	2.64	9.2	2.14
Aricidea suecica	2	0.59	0.1	0.02
Paraonis sp.	14	4.11	0.2	0.05
Chaetozone gayheadi	16	4.69	0.9	0.21
Chaetozone setosa	2	0.59	-	0.00
Dodaecaceria	1	0.29	-	0.00
(c.f.) Tharyx annulosus	1	0.29	-	0.00
Tharyx marioni	3	0.88	0.4	0.09
Tharyx sp.	8	2.35	-	-
Cirratulidae	8	5.28	42.4	9.86
Cossura sp.	1	0.29	0.1	0.02
Auchenoplax crinita	12	3.52	0.4	0.09
Glyphanostomum pallescens	7	2.05	6.1	1.42
Polycirrus medusa	8	2.35	88.8	20.65
Terebellidae	2	0.59	5.6	1.30
Chone duneri	2	0.59	1.7	0.40
Jasmineira bermudensis	8	2.35	3.2	0.74
Sabellariidae	1	0.29	0.2	0.05
Oligochaeta	12	3.52	0.2	0.05
Sipunculida				
Aspidosiphon sp.	10	2.93	2.6	0.60
Amphipoda				
Dedicerotidae	1	0.29	0.6	0.14
Genus sp. a	3	0.88	1.1	0.26
Genus sp. b	1	0.29	0.2	0.05
Genus sp. c	1	0.29	0.5	0.12

AII 79 Station 2027 (cont'd)

Group	Number of individuals	% comp	biomass (mg)	% biomass
Genus sp. e	3	0.88	0.3	0.07
Genus sp. f	2	0.59	0.2	0.05
Genus sp. g	1	0.29	0.6	0.14
Genus sp. L	8	2.35	9.1	2.12
Cumacea				
Campylaspis cf. horrida	2	0.59	0.4	0.09
Campylaspis sars	2	0.59	-	0.00
Diastylis sp.	1	0.29	0.4	0.09
Isopoda				
Sphaeroma quadridentatum	3	0.88	3.2	0.70
Tanaidacea	1	0.29	0.9	0.21
Ostracoda	1	0.29	0.4	0.09
Decapoda				
Betaeus sp.	8	2.35	-	0.00
Goneplacidae	8	2.35	121.0	28.13
Pycnogonida	9	2.65	-	-
Pelecypoda				
Nucellina sp.	1	0.29	0.8	0.19
Solemya sp.	8	2.35	0.4	0.09
bivalve b	2	0.59	0.2	0.05
Amphioxus	1	0.29	0.1	0.02

AII 79 Station 2028 grab A

Group	Number of invididuals	% comp	biomass (mg)	% biomass
Nematode				
Mesacanthion sp.	5	3.5	-	-
Oncholaimidae	2	1.4	-	-
Filoncholaimus n.sp.	76	53.5	-	-
Cyatholaimidae a	10	7.0	-	-
Cyatholaimidae b	2	1.4	-	-
Halichoanolaimus	3	2.1	-	-
Monhysteridae b	2	1.4	-	-
Polychaeta				
Lycastopsis sp.	3	2.11	0.6	3.24
Protodorvillea minuta	4	2.82	0.1	0.54
Stauronereis rudolphi	1	0.70	-	-
Aricidea jeffreysi	1	0.70	2.6	14.05
Aricidea neosuecica	2	0.70	0.1	0.54
Aricidea suecica	2	1.41	9.4	50.81
Aricidea quadrilobata	3	2.11	0.2	1.08
Cossura longocirrata	3	2.11	0.2	1.08
Oligochaeta				
species a	11	7.75	0.3	1.62
species b	12	7.04	0.2	1.08
Sipunculida	1	0.70	3.9	21.08
Amphipoda	1	0.70	0.4	2.16
Pelecypoda species b	1	0.70	0.5	2.72

AII 79 Station 2028 Grab B

Groups	Number of individuals	% comp	biomass (mg)	% biomass
Nematoda				
Anticoma sp.	4	1.46	-	-
Phanoderma sp.	4	1.46	-	-
Filoncholaimus n.sp.	52	18.98	-	-
(cf.) Vasostoma sp.	2	0.73	-	-
Chromadoridae	2	0.73	-	-
Neochromadora sp.	6	2.19	-	-
Pomponema sp.	6	2.19	-	-
Halichoanolaimus sp.	6	2.19	-	-
Desmocolecidae	2	0.73	-	-
(cf.) Tricoma	4	1.46	-	-
Monhysteridae a	10	3.65	-	-
Daptonema	4	1.46	-	-
Polychaeta				
Pilargidae	3	1.09	-	-
(cf.) Streptosyllis arenae	1	0.36	1.0	0.04
Langerhansia anoculata	5	1.82	0.6	0.26
Protodorvillia near Keferstei	7	2.55	0.2	0.09
Protodorvillia minuta	19	6.93	1.2	0.53
Ophyrotrocha	17	6.20	0.6	2.63
Stauronereis caecus	16	5.84	1.7	0.74
Questidae	1	0.36	-	-
Aricidea albatrossae	2	0.73	4.3	1.88
Aricidea bilgicae	3	1.09	0.3	0.13
Aricidea neosuecica	1	0.36	0.1	0.04

AII 79 Station 2028 Grab B

Group	Numbers of individuals	% comp	biomass (mg)	% biomass
Aricidea quadrilobata	1	0.36	1.9	0.83
Paraonis gracilis	5	1.82	0.6	0.26
Nathria pallidula	3	1.09	13.6	5.95
Nerinides near tridentata	2	0.73	3.1	1.36
Spiochaetopterus sp.	3	1.09	8.8	3.85
Oligochaeta				
species a	11	13.87	1.0	15.24
species b	9	3.28	0.6	0.26
Sipunculida				
Phascolion strombi	2	0.73	30.0	13.13
species a	1	0.36	2.2	0.96
Archiannelida	2	0.73	0.2	0.09
Decapoda				
Pagurina sp.	1	0.36	100.0	43.78
Pelecypoda				
species a	38	13.87	34.8	15.24
species b	18	6.57	15.0	6.57
species c	1	0.36	1.2	0.53

AII 79 Station 2029

Nematoda				
species a	1	50	-	-
species b	1	50	-	-

Station 4 Atlantis II cruise 86

Species	2	4	5	6	7
Nematoda					
Enoplidae sp. a		2			
Enoplidae sp. b				2	
Filoncholaimus sp.		4			3
Chromadoridae sp. a	2				
Halichoanolaimus sp.	14	12	19		5
Monhysteridae sp. a	36	53	50	22	50
Monhysteridae sp. b	27	27	39	18	29
Monhysteridae sp. c		8	4	4	8
Monhysteridae sp. d					5
question a	2	6	16		8
question b	5	2	4		
question c	4		23		13
question d		4	4		
question e			4		
Oligochaeta*	34	45	74	52	46
	5.2	7.0	8.5	8.6	7.0
Sipunculida					1
					7.3
Polychaeta	1.5	1.3			12.5
Spiochaetopterus sp.	7	8			6
	63.7	18.2	40.2	12.5	15.0
Cirratulidae sp. a		1		2	47
		0.6			9.0
Cirratulidae sp. b					41
					7.7
Dorvillidae			2		2
Flabelligeridae					1
					10.6
Nereidae			1		
			1.3		
Onuphidae		2			1
Paraonis sp.		3		3	7
		0.4	2	0.1	2.3

* Not used in diversity or percent similarity calculations.

Station 4 Atlantis II cruise 86 (cont'd)

Species	2	4	5	6	7
Aricidea jeffreysi	2 1.6				
Spiophones sp.		2 0.5	8 1.5	1	4 0.1
cf. Cossura longicirrata	1	4 1.1	1 0.7		1
Syllidae	1 1.0	1 1.0	1 0.8	2 2.7	
Pelecypoda	11	13	10		8
Leucindae	3.70	32.9	13.3		40.9
Lepiondae		6 77.4	2 3.1		4 103.0
gn sp c		1 81.5			1 21.1
Gastropoda		3			1
Gaza sp.		4.2			1.5
Amphipoda					
gn sp. a		1 4.0	1 0.4		1 1.5
gn sp. b			1 1.0		
Isopoda sp. a			1 5.0		

Appendix III

Species list from off Cap Blanc, Spanish Sahara

Species data are presented in the following format:

Species name	Sample
Species x	x
	y

x = number of individuals in 0.1 m^2 van Veen grab sample

y = biomass (mg) in 0.1 m^2 van Veen grab sample

Biomass only is given for fragments.

Numbers only are given for nematodes.

* Indicates organisms not included in diversity calculations.

Species name	162 1	162 2	162 3	163 1	163 2	163 3	165 1	165 3	166 1	166 2
Lenterata										
Delenterate gn sp				16				2		
				0.4				34.2		
ertea										
emertea sp a		4	4	48	16	16	16	10	4	8
		0.9	2.7	1.6	2.9	33.8	104	78.4	4.4	1.8
emertea sp b		4	4		16				4	
		131.8	26.2		5.6				3.7	
atoda										
hoanolaimus sp a				8						
hoanolaimus sp b				8						
halassironus sp							16			
hromadoridae sp b							32	4		
hromatodoridae gn sp									4	
yatholaimini sp				8						
esmoscolecidae sp							16			
esmoscolex sp				48						
orylamni sp					8					
oryonchus sp								4		
noplidae sp a				16						
noplidae sp c						32				
noplidea gn sp a							32			
noplidea gn sp b							16			
noplidea gn sp c							16			
udesmoscolex sp								4		
etalinhomaeus sp								4		
onhysteridae sp a				32				4		
onhysteridae sp b							32	4		
onocholaimus sp							16			
onysteridae gn sp		8	8						8	
ncholaimellus sp							16			
ncholaimus sp a							16			
ncholaimus sp b								4		
Polydontus sp						8				
Pseudonchaimus sp					8					
question a							16			
question b							16			
question c							16			
question d							16			
question e					8					
question f			32	8						
question g				32	8	16				4
question h				8						
question i				16						
question j								12		
(c.f.) Oncholaimellus						8				
Desmolaimus sp								4		
Tricoma sp								8		
nelid										
Archiannelid sp							64			

Species name	162 1	162 2	162 3	163 1	163 2	163 3	165 1	165 3	166 1	166 2
ychaeta ragments	440.0	226	151	263	318	247	1171	509	1.0	34
uphrosinidae gn sp			4 1.4							
hyllodocidae sp		4 8.4	8 3.9	16 7.5				2 0.6		8 1.2
esiondiae sp. (c.f.)				8		8 3.0				
ilargid gn sp				8 0.5						
utolytus sp						24 21.6			8 0.4	
xogone sp						72 3.2			4	
yllidae gn sp a	4 0.8			4 2.4	72 3.4	8 18.1	48 3.2	38 1.0	8 0.6	
yllidae gn sp b				8 1.2	8 1.4	24 3.2	32 1.6			
yllidae gn sp c							32 1.6	8 0.8		
yllidae gn sp d							16 3.2	32 0.8		
ereid sp a		12 1.4		16 2.4	8 5.6	8 0.8	48 40.0	34 1.6		
ereid sp b							32 46.4			
ephtyidae sp		16 31.7								
lyceridae sp	4	8 23.8		8 334.1	8 176.4	16 28.0	48 1419	2 138.6	4 0.1	
lyceridae sp b									4 55.1	
oniadidae gn sp						8 6.2				
nuphidae sp a		8 20.4	20 49.9	8 0.1	8 8.4	8 0.3	32 3.2		128 14.2	4
nuphidae sp b		4 1.3	4 0.3				32 387.2		8 42.6	
nuphidae sp c	24 34.8	4 22.0	4 3.2				32 344		20 2033.2	4 120
nuphidae sp d							16 2110	4 61.4	4 13.4	
nuphidae sp e							16 459.2	4 6.0		
umbrinereid sp	4 5.7	120 8.8	4 17.0	24 14.7	24 4.9		16 14.4		48 46.7	50
abellidae sp	8				8 2.3		16 12.8			
orvilleidae sp		4 3.8		24 0.1		72 9.4	16 3.2	26 63.6		

Species name	162 1	162 2	162 3	163 1	163 2	163 3	165 1	165 3	166 1	166 2
rbiniidae	4	20	12				16		16	4
	72.0	92.0	38.2				25.6		29.4	2.1
uestidae sp							48	16		
ricidea sp	4			16		8	48	2	4	
	0.4					2.6	102.4	1.2	1.0	
araonid sp a		12	16	16	24	24	128	16	4	
		4.6	2.8	0.8	1.0	2.3	73.6	0.3	0.3	
araonid sp b		8					48			
		3.4								
pistobranchidae sp		4	8							
		13.3	9.3							
ispio sp								4		
								2.4		
inuspio sp	24	24	44							
	28.8	17.8	70.0							
colelepis sp				8						
				0.6						
pio sp i										20
										4.5
pio sp a	28	84	80	1192	1112	1240	272	818	56	96
	1.2	8.5	9.2	109	86	53.6	163	617	9.8	15.0
pio sp b	24		56	169	96	40		408	36	52
	2.4		5.8	4.3	3.8	2.9		204.4	8.0	11.4
pio sp c	28				208	424	32	82	12	92
	11.2				29.8	49.5	1.6	24.8	3.9	27.2
pio sp d							32	394		
							12.8	155.2		
pionid sp b						240		74	12	
						37.4		92.0	1.0	
pionid sp d				64	24	16			4	
				7.3					0.9	
olydora sp.						40				
						6.0				
piophanes sp a		52		16		16				
		6.6		0.4		27.7				
.f. Spiophanes bombyx	4	24	12	8	24	40		44	20	36
	0.3	4.2	3.6	5.0	2.1	2.4		56.8	6.6	7.8
agelonidae sp		20	4							
		13.6	2.4							
piochaetopteridae		12	16							
		41.4	414.4							
irratulid sp b				16	24	200		16		
				5.0	10.1	27.4				
irratulid sp c				56		80				
				7.2		76.0				
irratulus sp	20	16	12	72	24	152	48	18	4	8
	4.1	1.3	1.2	15.6	2.2	65.5	16.0	4.4	0.1	7.0
haryx sp	8	8	12		40			4	16	8
	2.5	210.5	9.5		1063			15.8	3.6	5.0
ossura sp	20	96	36							
	0.4	4.8	1.9							
tenodrillidae sp	4									

Species name	162 1	162 2	162 3	163 1	163 2	163 3	165 1	165 3	166 1	166 2
Labelligeridae sp						8			8	
						2.8			86.0	
Labelligeridae sp b									4	
Ophiliidae sp		4	4	32		8			4	
		1.6	3.8	0.4		2.0			2.0	
Paldanid sp	4	8	12	8			16		4	12
	33.7	60.0	22.0	18.4			174.4		36.7	59.5
Pabellariidae gn sp			4							
			11.5							
Opharetidae sp a			4				16		4	
			25.6				6.4		17.4	
Opharetidae sp b		12	4						4	
		58.6	6.2						0.2	
Opharetidae sp c									4	
									0.4	
Perebellidae gn sp							16			
							2353			
Perebellidae gn sp b	12	4				8				
	50.0	44.1				0.8				
Pabellidae sp		8		8	8	8				
		6.1				8.0				
Trichobranchidae sp		4			8					
		0.7			7.7					
Poecilochaetidae sp							18		4	
							7.0		0.6	
Psaretidae sp						8				
						1.8				
Oligochaeta										
Oligochaeta sp						208	192	14		
						20.6	83.2	6.8		
Tanaidacea										
Tanaid sp a				8		8	32	4		
				812.1		3.4	6.4	1.2		
Decapoda										
Polemya sp					8					
					87.6					
Cf. Ensis sp									4	
									25.7	
Tellina sp	16	20	36						4	
	792.9	1506.9	1312						530.6	
Veneracia sp									16	
									216.3	
Cockle								2		
								11.6		
Venus sp a					8					
					1.2					
Venus sp b		4		8	8	8				
		1.7		1.0	10.4	87.6				
Venus sp c										4
										66.2
Ostracoda										
Ostracod sp			8	8	8	72		20		8
			7.9	0.2	44.8	7.9		2.0		2.0

Species name	162 1	162 2	162 3	163 1	163 2	163 3	165 1	165 3	166 1	166 2
epoda										
arpaticoid copepod				8		24		28		
				0.1		0.6		4.0		
acea										
umacea sp a			4		24	16		2	12	4
			0.8		11.3	0.3		0.2	0.6	0.1
umacea sp b					16			2		
					1.2			0.2		
umacea sp d								2		
								0.2		
iastylis sp								2		
								1.8		
aidacea										
anaidacea sp a	28	28	20		40	24		22	8	4
	230.8	2.0	26.4		2.1	2.4		55.4	3.6	
anaidacea sp b	12	8	20		16				4	
	13.3	14.5	1.7		11.4				0.1	
anaidacea sp c		4					16	4		
		27.0						5.0		
poda										
labellifera gn sp	4									
	2.0									
nathia sp	20	76		28						12
	5.1	6.9		6.4						4.3
sopod gn sp				8	8	8		2	4	4
				0.2		4.1		0.2		4.3
hipoda										
mphipod sp a	4	12		16	72	8	96	58	20	16
	9.2	18.8		5.4	3.6	6.6	26.3	18.2	1.5	11.4
mphipod sp b	8	4	4	8	8	8	32	14	16	16
	2.8	1.2	0.6	1.7	2.3	10.6	0.3	9.2	78.6	6.4
mphipod sp c		4	12	8	16	32	16	2	8	28
		1.6	6.3	0.8	3.9	2.7	13.9	0.6	0.5	6.7
mphipod sp d	4	4	20	8		8	16	2	4	28
	3.0	10.4	24.8			0.8		1.8		7.8
mphipod sp e	8	4		8		8	16	2	4	16
	14.0	2.0				1.0	4.8	0.2	1.2	27.6
mphipod sp f	4			8		24	144	2	4	4
	3.2			0.6		3.0	142.4	0.4	0.3	1.5
mphipod sp g						16	48	38	8	4
						2.0	68.8	0.1	0.6	0.5
mphipod sp h						8	16	2	4	4
						1.0	23.1	0.2	0.3	0.3
mphipod sp i						8	48	2	52	28
						1.0	0.3	0.8	16.8	13.8
mphipod sp j						8	16	18	12	4
						1.0	1.0		0.2	
mphipod sp k								18	8	4
								4.4	1.2	0.2
mphipod sp l									4	
									0.4	
apoda										
ragments		30.6								

Species name	162 1	162 2	162 3	163 1	163 2	163 3	165 1	165 3	166 1	166 2
ıgidae gn sp								2		
								8.6		
ıgurus brevidactylus			4							
			192.4							
ıgurus pollicarus		20	12							8
		163.6	160.4							293.2
ılicidae gn sp			4							
			93.2							
[nodermata										
:ndrochirota gn sp							10	4		
							2153	1166		
)hiuroidea fragments		8.6	49.6							
)hiuroidea								2	4	4
									1.2	5.9
:chin				40				22		
				4.1				2.6		
:data										
ıphioxus sp									16	40
									9.1	10.9

Appendix IV

Diversity and Evenness Values for Fosa de Cariaco and N.W. Coast of Africa excluding nematodes and oligochaetes (based on numbers)

	Station No.	Depth	H'(s)	E/S	No. indiv.	No. species
	2027	90	3.666	0.559	317	70
	2028a	202	2.244	0.857	21	11
	2028b	202	2.477	0.317	152	23
Fosa de	4-2	210	1.210	0.671	22	5
Cariaco	4-4	210	2.126	0.698	45	12
	4-5	210	1.967	0.596	43	12
	4-6	210	2.028	0.844	19	9
	4-7	210	1.805	0.405	128	15
	162-1	39	3.062	0.737	336	28
	162-2	39	3.333	0.501	876	54
NW Coast	162-3	39	3.184	0.619	564	37
of Africa	163-1	62	1.895	0.175	1989	37
	163-2	62	1.946	0.212	1984	32
	163-3	62	2.434	0.238	3096	47
	165-1	57	3.384	0.670	1756	43
	165-3	57	2.321	0.204	2334	49
	166-1	35	3.001	0.529	692	54
	166-2	35	3.371	0.574	674	34

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